THE GENERA OF ALYSSEAE (CRUCIFERAE; BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1,2]

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Tribe **Alysseae** A. P. de Candolle, Syst. Nat. **2:** 147, 280. 1821, "Alyssineae."

Annual, biennial, or perennial herbs [sometimes subshrubs, shrubs, or even trees]; usually with stellate, dendritic, cruciform, or furcate trichomes, rarely glabrous or with simple trichomes only. Inflorescences ebracteate [or bracteate], corymbose racemes, usually elongated in fruit. Sepals erect to spreading, strongly saccate at base or not saccate. Petals present or absent, undifferentiated or strongly differentiated into blade and claw. Nectar glands distinct or connate. Stamens usually 6, often tetradynamous; filaments with or without wings, teeth, or appendages. Fruits usually less than 3 times as long as wide, dehiscent [or rarely indehiscent], inflated or most commonly flattened parallel to the septum (latiseptate), sessile or long stipitate; valves usually 1-nerved, glabrous or with 1 or more types of trichome; septum present or absent; styles long to obsolete; stigmas entire to 2-lobed. Seeds 1 to numerous, usually biseriately arranged in each locule, mucilaginous or not when wet, broadly winged to wingless; funicles

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[2] For an account of the family and its tribes, see Al-Shehbaz, The tribes of Cruciferae (Brassicaceae) in the southeastern United States. Jour. Arnold Arb. **65:** 343–373. 1984.

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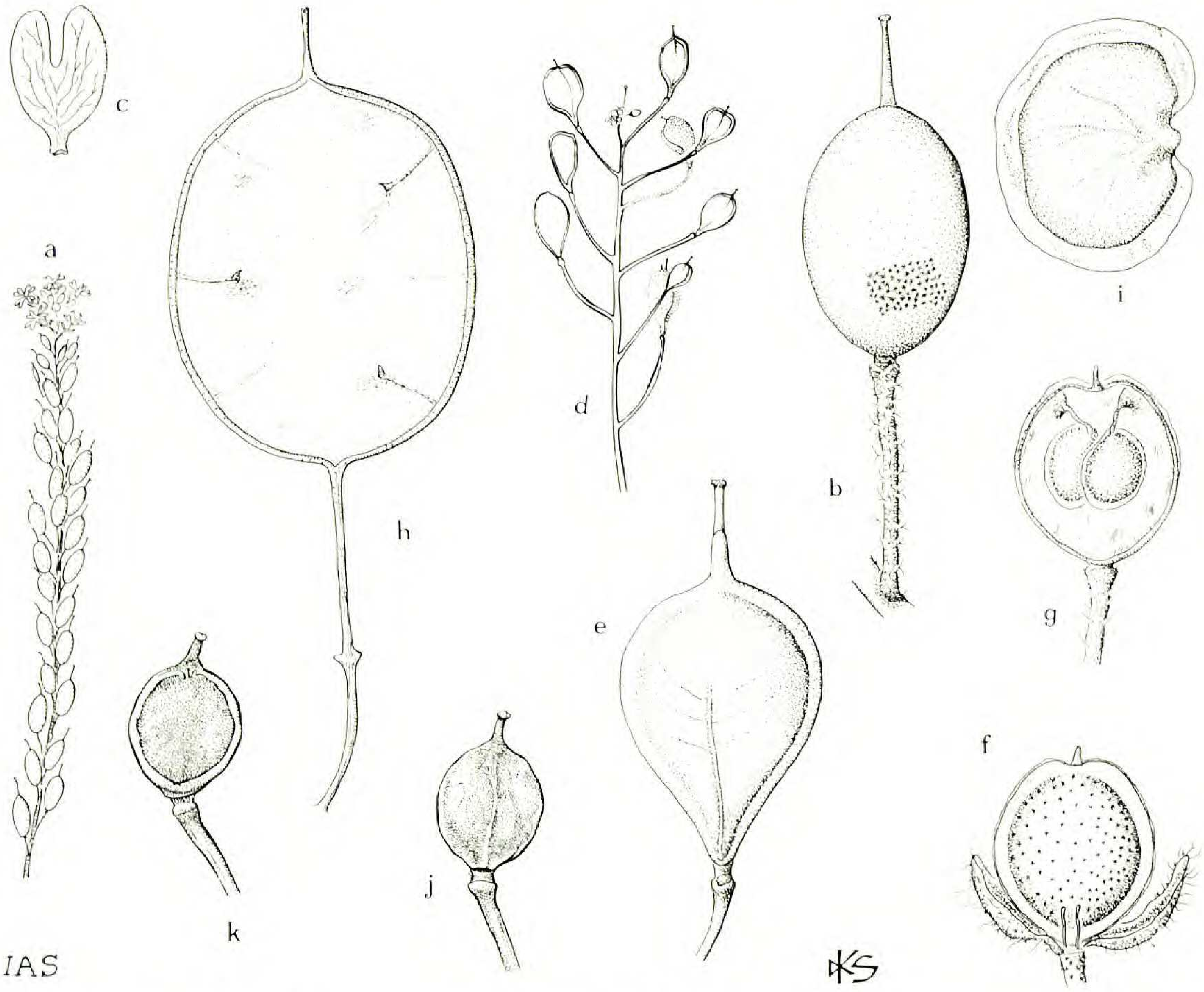

FIGURE 1. Selected representatives of tribe Alysseae. a–c, *Berteroa incana:* a, portion of plant with flowers and fruits, × ½; b, fruit with rectangular portion of valve showing trichomes, × 5; c, petal, × 5. d, e, *Camelina microcarpa:* d, portion of infructescence, × 1; e, fruit, × 5—note beaklike apex of valve. f, g, *Alyssum Alyssoides:* f, fruit with 1 persistent sepal removed, × 5—note filiform nectar glands; g, fruit with 1 valve and all sepals removed, × 5—note subapical placentae. h, i, *Lunaria annua:* h, septum and replum, × 1—note gynophore and adnation of funicles to septum; i, seed, × 3. j, k, *Lobularia maritima:* j, fruit, × 6; k, replum and septum, × 6.

free or adnate to the septum, apically or laterally attached to the replum; cotyledons accumbent. (Including Camelineae DC., Drabeae O. E. Schulz, Lunarieae O. E. Schulz.) TYPE GENUS: *Alyssum* L.

A poorly defined tribe with some 40 genera (15 monotypic) and about 650 species (excluding *Lesquerella* S. Watson) distributed primarily in the Irano-Turanian (ca. 210 species) and Mediterranean (ca. 110 species) regions. The majority of species belong to two genera: *Draba* L. (350) and *Alyssum* (170). Except for *Draba*, the Alysseae are poorly represented in Siberia, eastern Asia, and North America and are absent in the Southern Hemisphere and in the arctic and Himalayan regions. The tribe is represented in the southeastern United States by seven genera and 20 species, of which 13 are indigenous.

The limits of the Alysseae adopted here closely follow Janchen's classification, which unites the tribes Lunarieae, Drabeae, and Alysseae of Schulz. Janchen followed Von Hayek in treating the first two as subtribes of the last. Both *Selenia* Nutt. and *Armoracia* Gaertner, Meyer, & Scherb., which were placed by Schulz in the Lunarieae and the Drabeae, respectively, will be treated in the Arabideae DC., where their nearest relatives are usually placed. The South African *Schlechtera* Bolus, treated in the Lunarieae by Schulz, has diplecolobal embryos (with cotyledons twice transversely folded) and should therefore be included with its allies of the Heliophileae DC. *Lesquerella* was placed by Schulz in the Drabeae, but as is clearly shown below, it should be placed with its nearest generic relatives in the Lepidieae. However, it is treated here in the Alysseae, as shown in the outline adopted by Al-Shehbaz (1984).

Schulz separated the Lunarieae from the Alysseae mainly on the basis of simple vs. branched or stellate trichomes. Both *Ricotia* L. and *Peltaria* Jacq. (including *Leptoplax* O. E. Schulz), which he placed in the former tribe, have members with simple or branched trichomes, as do numerous other genera of the Cruciferae. Therefore, the type of pubescence alone cannot be used as the basis for tribal delimitation. Similarly, the cellular pattern of the fruit septum, considered by Schulz to be the main difference between the Alysseae and the Drabeae, is an unreliable feature and should not be overemphasized. Many authors (e.g., De Candolle, 1821, 1824; Von Hayek; Janchen) placed the core genera *Draba, Alyssum,* and *Lunaria* L., as well as their immediate relatives, in the tribe Alysseae, a disposition I presently support. It is clear, however, that the tribal classification of the Cruciferae is inadequate, and further studies may alter the boundaries of the Alysseae. Knights & Berrie found that data from sterols support the placement of *Lunaria* but not *Draba* in the Alysseae.

Chromosome numbers are known for some 275 species (ca. 43 percent of the tribe) and 28 genera (excluding *Lesquerella*). Nearly 80 percent of the species surveyed have chromosome numbers based on eight, and only about seven percent have numbers based on seven (author's compilation). About 50 percent of the species are diploid, and nearly 38 percent are exclusively polyploid. Polyploidy occurs in nearly 60 percent of the species of *Draba.* Aneuploidy and polyploidy probably played important roles in the evolution of *Lobularia* Desv. and *Hormathophylla* Cullen & T. R. Dudley.

The Alysseae are almost exclusively herbaceous; only a few species in three genera are woody. Some species of *Alyssum* and *Hormathophylla,* particularly those growing in the eastern Pyrenees, southern France, and eastern Spain, are subshrubs or shrubs to 50 cm high. *Farsetia* Turra has the most diversified habit of any genus of the Cruciferae. It includes several annual and perennial herbs, as well as subshrubs, shrubs, and even small trees. *Farsetia somalensis* (Pax) Gilg & C. Benedict (Somalia, Kenya, and Ethiopia) is a large shrub or small tree with hard wood and glossy, gray to red-brown bark, while *F. undulicarpa* Jonsell (Kenya and Tanzania) is a shrub to 2 m high (Jonsell, 1986).

The majority of the Alysseae have rather small seeds dispersed either by strong winds in open habitats or by rain wash. Wind dispersal is common in many genera with broadly winged seeds (e.g., *Farsetia, Fibigia* Medicus, *Lunaria*). It is restricted, however, to a few genera with samaroid (*Neotchihatchewia* Rauschert, *Peltaria*) or inflated (*Physoptychis* Boiss.) indehiscent fruits. Seeds that produce abundant mucilage when wet may be dispersed by adhering to animals. The fruits of two species of *Clypeola* L. (*C. lappacea* Boiss. and *C. aspera* (Grauer) Turrill) and of the monotypic *Asperuginoides* Rauschert (formerly *Buchingera* Boiss. & Hohen.; see Rauschert) are covered with glochidiate trichomes or deflexed barbellate spines and are dispersed by clinging to the fur of mammals.

Genera of the Alysseae in the southeastern United States are either noxious weeds or have members with weedy tendencies. Except for a few species of *Camelina* Crantz that are cultivated for their seed oils in parts of the Soviet Union and Europe, the tribe has no food value. Several species of *Alyssum, Aurinia* (L.) Desv. (golden-tuft alyssum), *Draba,* and *Lunaria* (honesty or money plant) are ornamentals cultivated on a limited scale. On the other hand, *Lobularia maritima* (L.) Desv. (sweet alyssum) is probably the most widely cultivated ornamental of the family Cruciferae.

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KEY TO THE GENERA OF ALYSSEAE IN THE SOUTHEASTERN UNITED STATES[4]

A. Fruits more than 1 cm wide, gynophores 1–5 cm long, funicles completely adnate to the septum; trichomes simple or lacking. .... 20. *Lunaria.*

A. Fruits less than 1 cm wide, gynophores absent or to 3 mm long, funicles free from the septum or adnate only at base; trichomes branched, sometimes mixed with simple ones.

  B. All trichomes uniformly bifurcate, medifixed, sessile, appressed. .... 22. *Lobularia.*

  B. Trichomes furcate, branched, or stellate, sometimes mixed with simple ones, stalked or sessile, usually appressed when stellate.

    C. Fruits inflated, not compressed, pyriform or globose to subdidymous.

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[4] The genera are numbered as in the treatment of the tribes of the Cruciferae in the southeastern United States (Jour. Arnold Arb. **65:** 343–373. 1984). Genera 1 and 2 (Thelypodieae) appeared in *ibid.* **66:** 95–111. 1985; genera 3–13 (Brassiceae) in *ibid.* 279–351; and genera 14–19 (Lepidieae) in *ibid.* **67:** 265–311. 1986.

D. Fruits pyriform, keeled at the replum, the valves acuminate, ending abruptly in a stylelike beak, the septum nerveless; seeds usually oblong, cotyledons incumbent. .... 26. *Camelina.*

D. Fruits globose to subdidymous, not keeled, the valves rounded or obtuse at apex, the septum (when present) with a midnerve extending from its center to the base of style; seeds nearly orbicular, cotyledons accumbent. .... 25. *Lesquerella.*

C. Fruits not inflated, compressed parallel to the septum, orbicular to oblong or lanceolate to linear.

E. Seeds 1 per locule, borne on an apical placenta, copiously mucilaginous when wet. .... 21. *Alyssum.*

E. Seeds 2 to many per locule, borne on 2 parietal placentae, not or only slightly mucilaginous when wet.

F. Cauline leaves strongly auriculate; fruits with bulbous-based trichomes, septum with a midnerve extending from its center to the base of style. .... 25. *Lesquerella.*

F. Cauline leaves usually not auriculate; fruits without bulbous-based trichomes, septum nerveless.

G. Petals deeply 2-lobed; filaments of lateral stamens appendaged; seeds winged or margined. .... 23. *Berteroa.*

G. Petals entire or sometimes emarginate, if 2-lobed (*Draba verna*) then plants scapose; filaments unappendaged; seeds neither winged nor margined. .... 24. *Draba.*

20. **Lunaria** Linnaeus, Sp. Pl. **2:** 653. 1753; Gen. Pl. ed. 5. 294. 1754.

Annual(?), biennial [or perennial] herbs with simple trichomes. Stems erect, branching above. Basal and lower cauline leaves opposite or rarely alternate, long petiolate, large, ovate-cordate, undivided, coarsely dentate [or spinulose-dentate]; upper leaves alternate, sessile or subsessile [or distinctly petiolate]. Inflorescences corymbose racemes or panicles, greatly elongated in fruit; lowermost branches bracteate; flowers ebracteate, large, showy. Sepals erect, cucullate; outer pair linear, not saccate at base; inner pair broadly oblong-elliptic, strongly saccate. Petals violet or purple, rarely lavender or white, obovate, long clawed, usually twice as long as the sepals or longer. Lateral nectar glands large, annular, 2-lobed on the outer side, 3-lobed on the inner [sometimes divided into inner and outer semiannular halves]; median glands absent. Stamens 6, tetradynamous; filaments linear, free, the bases terete or flattened, erect (median pairs) or strongly curved (lateral pair); anthers large, linear or oblong, obtuse. Ovary stipitate, 4- to 8-ovulate, glabrous or ciliate; style filiform; stigma 2-lobed, the lobes decurrent [or not], opposite the replum. Fruits dehiscent, very large (2–9 × 1–3.5 cm), strongly flattened parallel to the septum, usually pendulous, oblong to suborbicular [or lanceolate-elliptic], obtuse [or acute] at both ends; valves glabrous, flat, papery, finely or obscurely net veined, without a midnerve; styles long [or short], usually flattened near the base; replum ciliate or glabrous; septum persistent, shining, membranaceous, nerveless, very broad, with narrowly linear epidermal cells perpendicular to the long axis of fruit; funicles long, almost completely adnate to the septum; gynophores slender, 1–5 cm long [rarely obsolete or to 1 mm]. Seeds few, large, biseriately arranged in each locule, reniform or rarely suborbicular, flattened, slightly biconvex, minutely reticulate, brown, uniformly broad winged all around except at the wingless area of hilum, nonmucilaginous when wet; cotyledons accumbent, large. Base chromosome number 15. LECTOTYPE SPECIES: *L. annua* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2**: 190. 1913; see also Green and Maire for a later lectotypification (based on *L. rediviva* L.) that contradicts article 8 of ICBN. (Name from Latin, *luna,* moon, which the large, persistent, silvery septum of the fruit superficially resembles.)—HONESTY, MONEY PLANT, SATIN FLOWER, MOONWORT.

A genus of three species native to southern, central, and eastern Europe. Two species are grown as ornamentals, and these sometimes escape from cultivation. The third, *Lunaria Telekiana* Jáv., is a narrow endemic of northeastern Albania. It differs from the other species in having very short (to ca. 1 mm) gynophores, densely ciliate valve margins, and lateral sepals with longer (to ca. 2.5 mm) saccate bases. Both *L. annua* (*L. biennis* Moench, *L. inodora* Lam.), honesty, bolbonac, silver-dollar, penny flower, money plant, $2n = 30$, and *L. rediviva* (*L. odorata* Lam., *L. alpina* Berg.), money plant, $2n = 30$, are grown in North America. *Lunaria annua* has been reported as an escape from cultivation, but apparently not a naturalized one, in many states (including Arkansas and Georgia). It is easily distinguished by its biennial habit, oblong to suborbicular fruits with both apex and base obtuse, and subsessile or sessile upper cauline leaves. In the perennial *L. rediviva* the upper cauline leaves are petiolate and the fruits are usually elliptic-lanceolate with both apex and base acute. Of the two subspecies of *L. annua,* only the biennial subsp. *annua* is present in our area. Subspecies *pachyrrhiza* (Borbás) Hayek, a perennial with fusiform tubers, is distributed in Romania, the Balkan peninsula, and southern Italy.

Lunaria is most closely related to the eastern Mediterranean *Ricotia* (nine species), from which it differs in its coarser habit (stems to 16 dm high), undivided leaves, and stipitate fruits (1–)1.5–3.5 cm wide with a well-developed septum. Species of *Ricotia* are smaller plants to 4 dm high having pinnate or trifoliolate (very rarely undivided) leaves and sessile fruits 0.5–1(–1.5) cm wide with a very delicate septum that is sometimes lacking. Both genera were maintained in the Alysseae by De Candolle (1821, 1824), Bentham & Hooker, Von Hayek, and Janchen, but the last two placed them in subtribe Lunariinae Hayek. In Schulz's classification *Lunaria* and *Ricotia,* along with six other genera, are placed in the tribe Lunarieae, which was distinguished from the Alysseae only by the presence of simple instead of branched trichomes. Both types of trichome, however, are found in several genera of the Cruciferae, notably *Arabis* L., *Draba,* and *Sisymbrium* L. Dvořák (1971) suggested that the Lunarieae *sensu* Schulz, particularly *Lunaria,* represent an evolutionary line derived from an ancestor not very different from *Macropodium pterospermum* Schmidt Petrop. of the Thelypodieae Prantl. The Lunarieae are a heterogeneous assemblage in which some genera (e.g., *Selenia* Nutt. and *Thysanocarpus* W. J. Hooker) are clearly unrelated to *Lunaria.* Von Hayek's derivation of *Lunaria* from *Ricotia* needs careful evaluation, but it is evident that the two are more closely related to each other than to other genera of the Cruciferae.

The erect sepals, long claws of the petals, and flattened bases of the median staminal filaments of *Lunaria* form a long tube that makes the abundant nectar usually accessible to insects with proboscises longer than 1 cm. The butterflies *Vanessa* (Nymphalidae) and *Pieris* (Pieridae), the bees *Bombus* (Bombidae) and *Andrena* (Andrenidae), and the honeybee *Apis mellifera* (Apidae) are among the most common visitors of *Lunaria* flowers (Knuth). Self-pollination can be brought about effectively by small pollen-collecting insects because of the close proximity of the stigma to the median anthers. Insects with short proboscises can reach the nectar by poking holes through the base of the calyx.

Most chromosome counts for *Lunaria annua* and *L. rediviva* indicate $2n = 30$, but Dvořák & Dadáková and Polatschek reported $2n = 28$ for these species. The last author suggested that *Lunaria* is based on $x = 7$, while Dvořák (1971) speculated that the genus evolved through allopolyploidy from unknown ancestors with $x = 7$ and 8. The karyotype of *Lunaria* consists of small chromosomes, of which two (at least in *L. rediviva*) are believed to be B chromosomes (Manton). Failure to observe this pair may have led to deviant counts. Diploid and tetraploid counts based on $x = 15$ have been found in *L. rediviva* (Jankun).

Lunaria is unusual in the Cruciferae for its high concentrations of unique or very rare secondary compounds. It is rich in alkaloids, of which some are known only in this genus and at least six (lunarine, lunaridine, lunariamine, numismine, tetrahydrolunarine, and tetrahydrolunaridine) have been characterized. Isopropyl, 2-butyl, and 5-methylthiopentyl glucosinolates have been found in *L. annua,* and the last compound occurs in *L. rediviva* (Kjaer). The green parts of plants of the former species also contain 3-methylthiopropylglucosinolate (Cole). It has been suggested that the high concentrations of alkaloids in *Lunaria* may have evolved as an escape from crucifer-adapted pathogens or herbivores. The seed extract of *Lunaria* is the first reported source of *m*-carboxy–substituted aromatic amino acids among higher plants (Olesen Larsen). The unhydrolyzed seed extract of *L. annua* contains four amino acids and γ-glutamyl derivatives not discovered previously in nature.

Lunaria annua is an excellent source of long-chain monounsaturated acids, which constitute 90 percent of the total fatty-acid content. The seed oil is a potential source of erucic acid (42 percent) and contains 21 to 25 percent nervonic acid. The content of the latter acid is the highest reported for any seed oil (Wilson *et al.*, Mukherjee & Kiewitt).

Because the funicles are adnate to the septum, the seeds of *Lunaria* usually remain attached to the septum after the valves fall off. They are eventually detached as a result of the vibration of the septum and may glide away from the plant because of the presence of a broad wing. However, they sometimes adhere to the valves and can be carried away with them.

Lunaria annua has an absolute requirement of cold treatment (vernalization) for flowering. Stem elongation in rosette plants can be induced by the application of the gibberellic acids GA3 and GA7. However, the gibberellin treatment fails to induce flowering in nonvernalized plants (Zeevaart). Likewise, sprouts developed on callus or on petioles grown in sterile cultures do not flower unless vernalized (Pierik, 1967). Annual plants of *L. annua,* which is otherwise a biennial, have been obtained recently (Wellensiek, 1973).

Both *Lunaria annua* and *L. rediviva* are grown for their attractive flowers and particularly for their infructescences, which are used in dry bouquets after the removal of valves and seeds. Crisp stated that the seeds are occasionally used as condiments and the roots are eaten as a salad or cooked as a vegetable. The seeds of *L. annua* contain high levels of long-chain fatty acids, but the species has not been used as a source of industrial oils. Although both species may escape from cultivation, neither is a successful weed in the New World.

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21. **Alyssum** Linnaeus, Sp. Pl. **2:** 650. 1753; Gen. Pl. ed. 5. 293. 1754.

Annual [biennial or perennial] herbs [rarely subshrubs]. Stems erect to decumbent, usually branched at base [sometimes with sterile shoots and winter rosettes]. Indumentum of appressed, stellate trichomes with few [or many] branched [or unbranched] rays [or sometimes of lepidote trichomes]; simple or furcate trichomes present [or absent]. Leaves undivided, entire, attenuate, neither swollen nor persistent at base. Inflorescence an ebracteate, corymbose raceme [or panicle], elongated [or not] in fruit; fruiting pedicels divaricate [ascending, or reflexed]. Sepals equal [or unequal], free [or sometimes appearing connate because of interlocking trichomes at adjacent margins of sepals], persistent [or caducous], [inflated] or not, equal, not saccate at base, pubescent on outside, glabrous [or pubescent] on inside. Petals yellow [white, or rarely pink or lavender], obovate [or spatulate], emarginate [or entire], gradually [or abruptly] narrowed into claws, glabrous or sparsely [to densely] pubescent on outside; claws without [or rarely with] a basal appendage. Nectar glands 4, 1 on each side of the lateral stamens, filiform [globose, or triangular], median glands always absent. Stamens 6, somewhat tetradynamous; filaments wingless [or unilaterally or bilaterally winged], toothless and unappendaged [or variously toothed and/or appendaged], free [or rarely connate]; anthers small, introrse, acute or obtuse at apex. Ovary sessile, 2 [1 or 4–8]-ovulate; placentation apical [or rarely parietal]; stigmas capitate. Fruits dehiscent [rarely indehiscent], orbicular [oblong, elliptic, ovate, obovate, or obcordate], almost always flattened parallel to the septum, inflated in the middle [or throughout, or not inflated], emarginate or truncate [acute, or retuse] at apex, entire [rarely crenulate or undulate] at margin, pubescent [or glabrous]; valves nerveless; styles persistent, pubescent [or glabrous]. Seeds compressed, narrowly [to broadly] winged [or wingless], mucilaginous [or not] when wet; cotyledons accumbent [or incumbent]. Base chromosome number 8. (Including *Gamosepalum* Hausskn.

non Schlechter, *Meniocus* Desv., *Moenchia* Roth, *Odontarrhena* C. A. Meyer, *Psilonema* C. A. Meyer, *Ptilotrichum* C. A. Meyer, *Triplopetalum* E. J. Nyárády.) LECTOTYPE SPECIES: *A. montanum* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 154. 1913. (Name from Greek, *a,* not or privative, and *lyssa,* rabies or madness; the name was used for plants reputed in ancient times as a remedy for hydrophobia, as a cure for madness, and as a calmative for anger.)—MADWORT.

A well-defined, taxonomically difficult genus of at least 170 (probably to 190) species primarily centered in Turkey (90 species, 50 endemic), with a rich representation in the Balkan peninsula (45 species, 20 endemic) and in the Caucasus and adjacent parts of the Middle East (63 species, 25 endemic). The genus is poorly developed in central and eastern Asia (seven species endemic) and in North Africa and the Iberian peninsula (eight endemic). With the exception of *Alyssum americanum* Greene (Alaska and Yukon Territory, Canada), which may be conspecific with the Siberian *A. obovatum* (C. A. Meyer) Turcz. (Dudley, 1964b), the genus is almost exclusively Eurasian and is mostly confined south of the 50th parallel. The great majority of taxa are narrowly endemic, and only about ten species are widely distributed weeds. *Alyssum* is represented in North America by one indigenous and six naturalized species, and in the southeastern United States by one weedy species.

Alyssum is divided into at least six or seven well-marked sections previously recognized as distinct genera. Section PSILONEMA (C. A. Meyer) J. D. Hooker (*Psilonema, Alyssum* subg. *Tetratrichia* Gay) (annuals; filaments slender, edentate, unappendaged, wingless; fruits dehiscent, valves equally inflated; seeds 2 per locule, winged or wingless, mucilaginous when wet), containing five species indigenous to southwestern Asia and the Mediterranean region, is represented in our area by a single species. *Alyssum Alyssoides* (L.) L. (*Clypeola Alyssoides* L., *C. campestris* L., *A. calycinum* L., *A. campestre* (L.) L., *Psilonema Alyssoides* (L.) C. A. Meyer), pale alyssum, $2n = 32$, a native of northern Africa and western Europe eastward to India, is naturalized in Canada, the United States, and Argentina. It grows on disturbed gravelly or sandy banks, waste grounds, and dry hillsides, in meadows, and along roadsides. It is rare in the Southeastern States and occurs in Cumberland County, Tennessee (R. Simmers, pers. comm.), Marion County, Arkansas (Smith), and Lincoln Parish, Louisiana (Logan). According to MacRoberts, the record from Louisiana needs verification.

Of the two varieties recognized by Dudley (1965a) in *Alyssum Alyssoides,* only var. *Alyssoides* is naturalized in the New World. The other, var. *depressum* (Schur) T. R. Dudley, is endemic to the Balkan peninsula. The species is distinguished from the other alyssums in North America by its persistent sepals; the compressed margin and inflated center of its fruits; its filiform, persistent nectar glands; and its unappendaged, toothless, and wingless staminal filaments. It may be confused with *A. desertorum* Stapf, but this has dentate filaments, deciduous sepals, and glabrous fruits.

Section ALYSSUM (annuals, biennials, or perennials; filaments winged, appendaged, or toothed; fruits dehiscent; seeds 2 per locule, winged or wingless, mucilaginous when wet), contains more than 70 species and is represented in North America by the Eurasian *A. desertorum, A. minus* (L.) Rothm. var. *micranthum* (C. A. Meyer) T. R. Dudley, *A. strigosum* Banks & Solander, and *A. Szowitsianum* Fischer & Meyer. These are naturalized in Manitoba and Alberta southward into the Mountain and Pacific states and Nebraska.

Section ODONTARRHENA (C. A. Meyer) W. D. Koch (perennials; filaments winged, dentate, or appendaged; fruits dehiscent or indehiscent, 1-seeded; seeds winged or wingless, rarely mucilaginous when wet) contains more than 70 species, of which only the native *Alyssum americanum* (= *A. obovatum*?) and the European *A. murale* Waldst. & Kit. grow in North America. The latter is an occasional escape from cultivation and is known from a few localities in Colorado, Michigan, and Québec.

The remaining sections of *Alyssum* (sects. MENIOCUS (Desv.) J. D. Hooker (seven species), GAMOSEPALUM (Hausskn.) T. R. Dudley (ten species), and TETRADENIA (Spach) T. R. Dudley (three species)) are not represented in North America. Krasnoborov has recently proposed the monotypic sect. STEVENIOIDES, which resembles sects. PSILONEMA and ODONTARRHENA in its edentate staminal filaments and uniovulate locules, respectively.

Both *Aurinia saxatilis* (L.) Desv. (*Alyssum saxatile* L.), golden-tuft alyssum, basket-of-gold, gold-dust, rock madwort, and *Au. petraea* (P. Ard.) Schur (*A. petraeum* P. Ard.) are occasional escapes from cultivation in the United States, and the former has been reported from Mississippi (Jones). Although *Aurinia* Desv. has been treated as a section of *Alyssum* by numerous authors (e.g., Busch, Schulz, Ball & Dudley, Maire, Markgraf), Dudley (1964c) recognized it as a genus remotely related to *Alyssum* and most closely allied to *Berteroa* DC. or possibly to *Alyssoides* Miller. Dudley separated *Aurinia* from *Alyssum* mainly on the basis of leaf characters. *Aurinia* was said to have repand-sinuate or dentate rosette leaves 2–10 cm long, deeply grooved petioles with swollen and persistent bases, and cauline leaves about half (or less) the size of the rosette ones. On the other hand, *Alyssum* has entire rosette leaves 0.5–2 cm long, flat petioles neither swollen nor persistent at the base, and cauline leaves subequal in size to the basal ones. These alleged differences, however, are inconsistent within each of the two genera. For example, the basal leaves of *Au. corymbosa* Griseb. and *Au. halimifolia* (Boiss.) Cullen & T. R. Dudley are usually entire and have petioles neither swollen nor persistent, while several species of *Alyssum* (e.g., *A. aizoides* Boiss.) have persistent and swollen petiole bases, and many others (e.g., *A. argenteum* All. and *A. Bertolonii* Desv.) have deeply grooved petioles. The other differences listed by Dudley, particularly the shape of floral buds and the lobing of immature stigmas, are not sharply defined and are therefore unreliable. All species of *Aurinia* have spreading sepals, while all except a few species of *Alyssum* (e.g., *A. spinosum* L.) have erect ones. *Aurinia* consists of closely related species that are difficult to separate from *Alyssum* on the basis of fruit and floral characters alone. The differences in leaf characters between these genera may not justify the recognition of *Aurinia* as an independent genus remotely related to *Alyssum.* The lack of reliable differences between these genera has led to the reduction of the former to a section of the latter, as was done by numerous authors including Ball & Dudley.

Alyssum is easily distinguished from other members of the Alysseae by its nonsaccate sepals, entire or inconspicuously lobed stigmas, appressed stellate trichomes occasionally mixed with furcate (but never medifixed and bifid) ones, and usually dehiscent and latiseptate fruits without barbulate trichomes. The genus is often confused with *Lobularia,* but this always has bifid, medifixed, appressed trichomes.

Very high rates of selfing have been observed in several species of *Alyssum* (Persson). Cleistogamy is often associated with damp weather. Günthart suggested that the basal wings, teeth, or appendages of staminal filaments guide the proboscis of a visiting insect to the nectar glands. Dudley (1963) and Bergdolt, on the other hand, claimed that these staminal structures are not involved in pollination, and the latter maintained that they are vestiges of ancestral petaloid structures from which the filaments evolved. It is highly unlikely, however, that these floral structures, which are present in all except five species of *Alyssum* and in several other genera of the Alysseae, do not participate in pollination and do not have adaptive value. It should be noted that the distinctions between certain sections of *Alyssum* and between certain genera of the Alysseae rely primarily on the presence vs. absence of the staminal appendages or teeth (Dudley, 1964b; Dudley & Cullen).

Chromosome numbers are known for about 90 species of *Alyssum,* and all except a few are based on eight. Species with deviating base numbers (e.g., *A. hirsutum* Bieb., $2n = 46$) most likely evolved through aneuploidy from ancestors with $x = 8$. Section TETRADENIA *sensu* Dudley (1964b) is the most cytologically heterogeneous of all sections of *Alyssum.* On the basis of chromosome numbers, morphology, and geographic distributions, Küpfer has transferred its three species, *A. spinosum* ($2n = 16$, 32), *A. cochleatum* Cosson & Durand ($2n = 22$), and *A. Lapeyrousianum* Jordan ($2n = 30$), to *Hormathophylla.* Diploid and tetraploid counts based on eight are known for *A. obovatum* from Siberia (Goldblatt, 1981, 1984, 1985). Recent counts of $2n = 30$ for *A. americanum* from Alaska (Dawe & Murray) may support its recognition as a distinct species, instead of its reduction to a synonym of *A. obovatum,* as was suggested by Dudley (1964b). At least 50 species are diploid, 20 are polyploid, and 20 have both diploid and polyploid populations. Polyploidy played an important role in the evolution of *Alyssum,* as is evidenced by its occurrence in about 45 percent of the species for which counts are known. Dudley (1963), however, found polyploidy in only two of the 21 species he compiled and suggested that it was insignificant in the evolution of the genus.

Persson studied the karyotypes of several species of *Alyssum* and noted that members of sect. ALYSSUM have rod-shaped chromosomes, while *A. Alyssoides* has elliptic ones. He suggested that *A. siculum* Jordan ($2n = 48$) is an intersectional allopolyploid hybrid, the parental species of which are *A. Alyssoides* and *A. minus* ($2n = 16$). Interspecific hybridization is apparently very rare in the genus.

Little is known about the chemistry of *Alyssum*; only eight species have been surveyed for fatty-acid composition, and eight others for glucosinolates. The limited data indicate that linolenic acid is the primary seed-oil constituent (39–66 percent), that oleic and linoleic acids are secondary (9–24 percent each), and that erucic acid is lacking (Kumar & Tsunoda). Methionine-derived glucosinolates, particularly 5-methylthiopentyl, 5-methylsulfinylpentyl, 3-methylsulfinylpropyl, and 3-butenyl glucosinolates, are the dominant compounds (Hasapis *et al.,* Kjaer). The distribution of seed glucosinolates and fatty acids does not support the maintenance of *Aurinia* as a genus distinct from *Alyssum,* but that of seed sterols apparently does (Knights & Berrie).

Vaughan & Whitehouse indicated that seed-coat anatomy supports the sectional classification of *Alyssum.* They found that in *Aurinia* (treated as a section) the epidermal cells have no central columns, the subepidermis is present, and the palisade cells have thickened radial and inner tangential walls. In *Alyssum* the epidermis contains large and hollow central columns, the subepidermis is lacking, and the palisade cells either have only the inner tangential walls thickened or have all walls evenly thickened. However, they surveyed only five percent of the species of *Alyssum,* and it is not known whether their observations hold for the rest of the genus. According to Metcalfe & Chalk, the stems of *A. spinosum* are composed of alternating concentric rings of small, unlignified, spirally thickened vessels and large, lignified ones with horizontal bordered pits. It appears that the vascular cambium periodically produces the "juvenile" form of xylem.

Most species of *Alyssum* have dehiscent fruits with small, usually mucilaginous, and often winged seeds. The seeds are dispersed either by wind or (when wet) by adhering to animals and equipment. In sect. ODONTARRHENA subsect. *Samarifera* T. R. Dudley (nine species; Turkey, northern Syria, and Lesbos Island, Greece) the fruits are modified into indehiscent, thin-walled, one-seeded samaras borne on slender, brittle, usually deflexed pedicels and are therefore dispersed by wind. The evolution of this type of dispersal was accompanied by an increase of fruit size.

Several species of *Alyssum* (e.g., *A. Szowitsianum*) have conical infructescences, the lowermost pedicels of which are two to three times longer than the upper ones. The pedicels are closely appressed to the rachis, but soon after their exposure to rain, they spread horizontally, displaying the concave valves upward. The impact of raindrops eventually leads to the detachment of the valves and the release of mucilaginous seeds. The anatomical basis for this hygrochastic movement of the fruiting pedicels was studied by Zohary & Fahn. They showed that the adaxial side of the swollen bases of the pedicels consists of thick-walled fibers with transversely arranged pores, while the abaxial side has thin-walled fibers with diagonally arranged pores. Due to water absorption by the thick-walled fibers, the bases of the pedicels swell further and consequently spread in a purely mechanical way.

Species of *Alyssum* occupy diverse habitats, but the majority are distributed in arid or semiarid areas. More than 50 percent of the species, particularly members of sects. ALYSSUM and GAMOSEPALUM, occur primarily on calcareous soils. Those of the latter section often grow on soft calcareous substrates, especially chalks, and rarely on gypsum. Most species of sect. ODONTARRHENA are endemic to serpentine and other ultrabasic substrates, and at least 46 (66 percent) are hyperaccumulators of nickel. Nickel levels in these species are often higher than 1000 μg/g of dry weight. The physiology of tolerance and hyperaccumulation of nickel is directly related to the presence of high levels of malic and malonic acids. Nickel is accumulated in the cell vacuoles, and its presence in the mitochondria is believed to block the citric-acid cycle by deactivating malic acid dehydrogenase. This deactivation leads to the buildup of malic acid in the vacuoles, enabling them to absorb more nickel (Brooks *et al.*, 1981a). Seeds of the hyperaccumulators of the *A. serpyllifolium* Desv. complex (Iberian peninsula) can germinate on soils with nickel concentrations up to 12,000 μg/g, while those of the nonaccumulators can only germinate at concentrations below 60 μg/g. These physiological differences support the treatment of each of the three subspecies of *A. serpyllifolium* as a distinct species.

Except for a few weedy species, the genus has little economic importance. *Alyssum murale,* silver alyssum, is cultivated as an ornamental in parts of Europe and North America. The ancients used an infusion prepared from the flowers and leaves of some species as a sedative for anger and a cure for rabies.

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22. **Lobularia** Desvaux, Jour. Bot. II. **3**: 162. 1815, nom. cons.[5]

Annual or perennial canescent herbs [rarely subshrubs], densely to sparsely covered with a uniform indumentum of sessile, appressed, bifid, medifixed trichomes. Stems erect to prostrate, branched from the base or above. Leaves entire, short petiolate, linear, oblong, lanceolate, or spatulate, always attenuate at base. Inflorescences terminal, usually ebracteate (or the lowermost flowers subtended by leaflike bracts), densely flowered, corymbose racemes, usually greatly elongated in fruit. Sepals oblong or ovate, obtuse, always spreading, equal, not saccate at base, densely pubescent. Petals white or rarely pink or purple, clawed, suborbicular to spatulate or obovate, entire, about twice as long as the sepals. Nectar glands 8, filiform to subclavate; median glands 4, 1 outside each median stamen; lateral glands smaller, 1 on each side of lateral stamens. Stamens 6, tetradynamous; filaments free, strongly dilated at base, toothless, neither appendaged nor winged; anthers ovate. Ovary pubescent, 2- [to 12-]ovulate; ovules on subapical [or parietal] placentae. Fruits dehiscent, flattened parallel to the septum, sessile or short stipitate, elliptic, ovate, orbicular, [oblong, or obovate]; valves obscurely nerved, glabrous or pubescent; styles persistent, short; stigmas capitate. Seeds 1 [2–6] per locule, narrowly [to broadly] winged, compressed, minutely reticulate, mucilaginous when wet; cotyledons accumbent. Base chromosome numbers 11, 12. (Including *Konig* Adanson, *Aduseton* Adanson, *Koniga* R. Br., *Glyce* Lindley.) TYPE SPECIES: *Clypeola maritima* L. = *L. maritima* (L.) Desv. (Name from Latin *lobulus,* a little lobe, referring to the small fruit, but some authors (e.g., Fernald) maintain that the name probably refers to the 2-lobed (bifid) trichomes.)—SWEET ALYSSUM.

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[5] The year of publication has been wrongly given in all floras as 1814. According to Stafleu & Cowan's Taxonomic Literature (Regnum Veg. **94**: 634. 1976), the year of publication of the above page of Desvaux's Journal was 1815. *Lobularia* is conserved, and the earlier generic names *Aduseton* and *Konig* of Adanson (Fam. Pl. **2**: 420. 1763) are rejected because the last name was not Latinized and *Aduseton* was spelled in two ways by Adanson, who added further confusion in his prefatory errata (p. 23) by transposing these names.

A genus of four species distributed primarily in the Mediterranean region and the Macaronesian archipelago (Azores, and the Salvage, Canary, and Cape Verde islands). One species, *Lobularia maritima* (L.) Desv. (*Clypeola maritima* L., *Alyssum maritimum* (L.) Lam., *Koniga maritima* (L.) R. Br., *A. minimum* L.), sweet alyssum or alison, $2n = 24$, is an ornamental widely cultivated throughout the world, an escape from cultivation, and a naturalized weed in the southeastern United States. It grows in waste places and lawns and on cultivated grounds in the Carolinas, Florida, Tennessee, Mississippi, and Louisiana. *Lobularia maritima* is an annual or perennial herb under cultivation, but in its native habitat in the Mediterranean region, Madeira, and the Canary Islands, where it occupies sea cliffs or sandy areas at sea level, it is always a perennial with a woody base and is sometimes a subshrub.

Earlier authors (e.g., De Candolle (1821, 1824), Bentham & Hooker, Baillon) treated *Lobularia* as a subordinate (often as a section) of the closely related *Alyssum.* There are, however, several morphological differences that support its treatment as a distinct genus. *Lobularia* has bifid trichomes, eight nectaries characteristically arranged (see above), spreading sepals, and toothless and unappendaged staminal filaments. *Alyssum* always has stellate trichomes, a different arrangement of the nectaries, toothed or appendaged filaments (except in five species of sect. PSILONEMA), and erect sepals (except in a few species). Two other genera of the Alysseae, *Farsetia* and *Bornmuellera* Hausskn., have trichomes similar to those of *Lobularia,* but they are easily separated by their dentate staminal filaments and strongly 2-lobed stigmas, respectively.

The identification of species of *Lobularia* relies heavily on the number of seeds per locule and on habit. Fragmentary specimens that lack mature fruits are often difficult to identify. As in several other genera of the Cruciferae, woody habit may have evolved in connection with insular isolation. All of the five taxa occurring in the Macaronesian archipelago are suffruticose perennials and under favorable conditions often become subshrubs. Annual habit, which is considered by Borgen (1984) to be derived in the genus, is found in two desert species, *L. arabica* (Boiss.) Muschler (Egypt, Israel) and *L. libyca* (Viv.) Meisner (Canary Islands, southern Spain, all of North Africa, Israel, and southern Iran). *Lobularia libyca,* the most widely distributed species in the genus, has the largest fruits, with up to six seeds per locule. *Lobularia maritima,* on the other hand, has the smallest fruits, with only one seed per locule. The fourth species, *L. intermedia* Webb & Berth., is intermediate between *L. maritima* and *L. libyca* in fruit size and in the number of seeds per locule. It is highly polymorphic, particularly in leaf morphology, fruit shape, and seed number. It was subdivided into several poorly defined varieties, the identities of which need critical evaluation. *Lobularia spathulata* (J. Schmidt) O. E. Schulz (Cape Verde Islands), *L. marginata* Webb & Berth. (high crests of the Anti Atlas Mountains, Morocco, and of Lanzarote and Fuerteventura, Canary Islands), and *L. palmensis* Webb ex Christ (eastern Canary Islands) are separated from *L. intermedia* on the basis of minor characters. They can be hybridized easily with each other and with *L. intermedia,* and the first generation hybrids show pollen fertility higher than 80 percent (Borgen, 1984). Therefore, they should be recognized as infraspecific taxa of *L. intermedia.*

Consistent counts of $2n = 24$ were reported for *Lobularia maritima* from many Mediterranean countries. However, Borgen (1984) also recorded $2n = 22$ and observed meiotic irregularities such as univalent and multivalent formations, chromosomal bridges, and lagging chromosomes. On the basis of these meiotic irregularities, particularly the frequent occurrence of univalents, Borgen (1984) suggested that *L. maritima* is probably an allopolyploid, but he did not indicate what its ancestral species were. He considered *L. maritima* to be the most primitive member of the genus despite its 1-seeded fruits that are the smallest in *Lobularia.* This species and the *L. intermedia* complex are self-incompatible, large-flowered, suffruticose perennials, whereas *L. libyca* and *L. arabica* are autogamous, small-flowered annuals. Uniform counts of $2n = 22$ have been reported for members of the *L. intermedia* complex, as well as for *L. libyca* (Borgen, 1970, 1974, 1984; Larsen). The count of $n = 6$ for *L. libyca* by Negodi may be an error. Snogerup and Borgen (1984) reported $2n = 46$ and $2n = 42$, respectively, for *L. arabica.*

Seed-coat anatomy of *Lobularia maritima* differs from that of *Alyssum* in the cell-wall thickening of the palisade layer. In *Lobularia* the cells are thin walled, while in *Alyssum* they are either evenly thickened throughout or the radial and/or inner tangential walls are thickened (Vaughan & Whitehouse).

Only *Lobularia maritima* has been surveyed for seed glucosinolates and fatty acids. High concentrations of 3-butenylglucosinolate, smaller amounts of 6-methylthiohexyl and 4-pentenyl glucosinolates, and traces of allyl, benzyl, and 2-phenylethyl glucosinolates were identified (Hasapis *et al.*). Kjaer & Gmelin found 5-methylsulfinylpentylglucosinolate to be the major component of the species. Although the fatty-acid composition of *L. maritima* resembles that of *Alyssum* in lacking erucic acid, it is markedly different in its high concentrations (42 percent) of eicosenoic acid and small amounts (10 percent) of linolenic acid. *Alyssum* contains only traces (0.4 percent or less) of the former acid and 36–66 percent of the latter (Kumar & Tsunoda). These observations, however, are based on an incomplete sampling of both genera.

Lobularia maritima growing in its natural habitats is highly variable in habit, leaf succulence, and resistance to salinity. Seashore populations are low-growing, bushy plants with broad, thick leaves and are resistant to salinity; inland ones are taller and generally erect plants with thin, linear leaves and are intolerant of salinity (Catarino *et al.*). Leaf succulence can be induced experimentally by prolonged treatment with 0.2 *M* sodium chloride. Such treatment increases the cell volume, nucleus size, and DNA content (often accompanied by endopolyploidy) in both palisade and spongy parenchyma (Capesius & Loeben).

Earlier literature indicates that *Lobularia maritima* was used as an astringent, an antiscorbutic, a diuretic, and a febrifuge. The species is the most widely cultivated of any ornamental crucifer. It is grown as a border plant and has sweet-smelling, white or purple flowers. It is also a naturalized weed in many parts of the world.

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23. **Berteroa** A. P. de Candolle, Syst. Nat. **2:** 290. 1821.

Annual or perennial herbs, densely pubescent with stellate trichomes mixed with fewer simple or bifid ones. Basal leaves petiolate, entire or occasionally repand or sinuate; upper cauline leaves sessile, entire. Inflorescences ebracteate, densely flowered, corymbose racemes, greatly elongated in fruit; fruiting pedicels erect-ascending [or divaricate], straight or curved. Sepals ascending to spreading, oblong, not saccate at base, densely pubescent, with or without a subapical tuft of simple trichomes. Petals white [or yellow], attenuate into a clawlike base, deeply emarginate, the sinus extending to nearly half the length of blade. Lateral nectar glands 4, 1 on each side of each lateral stamen; median glands absent. Stamens 6, tetradynamous; lateral filaments with a basal, adaxial appendage; median filaments dilated at base, neither appendaged nor winged;

anthers oblong, slightly exserted. Fruits sessile, 1–3 times as long as broad, elliptic, oblong, ovate [or orbicular], compressed parallel to the septum; valves with obscure midvein, inflated [or not], densely pubescent with appressed stellate trichomes [or glabrous]; styles persistent; stigmas capitate, obscurely 2-lobed, wider than the style. Seeds 2–6 per locule, compressed, suborbicular to obovate, margined [or conspicuously winged], nonmucilaginous when wet; cotyledons accumbent. Base chromosome number 8. (Including *Myopteron* Sprengel.) LECTOTYPE SPECIES: *Alyssum incanum* L. = *B. incana* (L.) DC.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 153. 1913. (Name honoring Carlo Giuseppe Bertero, Oct. 14, 1789–April 9, 1831, Italian physician and botanist of Piedmont, who traveled in the West Indies (1816–1821), settled in Chile in 1827, and died in a shipwreck in the southern Pacific.)—HOARY ALYSSUM.

A genus of five species centered in the Balkan peninsula and distributed from central Europe eastward into Turkey and the Caucasus. A few authors expand the limits of the genus to include *Berteroa spathulata* (Stephan ex Willd.) C. A. Meyer (central Asia and western Siberia), *B. Potaninii* Maxim. (Mongolia), and *B. macrocarpa* Ikonn.-Galitz. (Mongolia and central Asia). However, these are morphologically different and geographically disjunct from the remaining species of *Berteroa*. They have been transferred recently to a new segregate, *Galitzkya* V. Bocz., which differs from *Berteroa* in its subscapose habit, unappendaged filaments, and uniform pubescence.

Berteroa is represented in North America by two naturalized weeds, one of which is sporadic in the southeastern United States. *Berteroa incana* (L.) DC. (*Alyssum incanum* L., *Farsetia incana* (L.) R. Br., *Draba cheiranthifolia* Lam.), hoary alyssum, $2n = 16$, usually grows on dry sandy or gravelly soils in meadows, pastures, waste places, and fields, as well as along roadsides, railroad tracks, streams, and riverbanks. It was probably introduced into North America with either grass or clover seeds or in ballast (Martindale). Although *B. incana* was recorded from Tennessee as early as 1901 (Gattinger), it has been reported only recently from Arkansas, Kentucky, and Virginia. It is most abundant in the northeastern United States and is noxious in Minnesota and Michigan.

Berteroa mutabilis (Vent.) DC. is sporadically distributed in the United States and is naturalized in parts of Massachusetts, New York, and Kansas. Brooks's record of *B. obliqua* (Sibth. & Sm.) DC. from the Catskill region, New York, is based on a misidentified plant (*True 78*, NYS!) of *B. incana*. The former grows only as a native in Italy and the Balkan peninsula. The remaining species of the genus, *B. Gintlii* Rohlena and *B. orbiculata* DC., are endemic to Yugoslavia and the Balkan peninsula, respectively.

Although some earlier authors (e.g., Bentham & Hooker, Baillon) reduced *Berteroa* to a section of *Alyssum*, the two genera are not closely related. Von Hayek suggested that *Berteroa* is directly derived from *Fibigia*, while Schulz placed it between *Lobularia* and *Lepidotrichum* Velen. & Bornm. (= *Aurinia*). Obviously, the relationships between these and several other genera of the Alysseae have not been fully established. *Berteroa* is distinguished by its deeply bifid petals, appendaged lateral staminal filaments, mixed indumentum of stellate and bifid trichomes, and two to six seeds in each locule.

Very little is known about the floral biology of the genus. Knuth indicated that *Berteroa incana* is protogynous. Autogamy occurs as a result of contact between the median anthers and the stigma. In Europe the species is pollinated by several species of flies, particularly of the genera *Eristalis, Rhingia, Syritta,* and *Syrphus,* as well as by species of the butterfly genus *Vanessa* and the bee *Halictus.* Bateman listed one species of *Berteroa* (without name) as self-incompatible.

Chromosome numbers are known for all species except *Berteroa Gintlii.* The genus is uniformly based on $x = 8$, and all species are diploid. No interspecific hybridization has been reported.

The seeds of *Berteroa incana* contain very high concentrations (89 percent) of C_{18} fatty acids, of which linolenic acid is the major constituent (48 percent), and no traces of erucic acid (Appelqvist). Goering and colleagues considered the species to be agronomically acceptable and a good source of drying oils. The seedlings have large and small amounts of benzyl and isopropyl glucosinolates, respectively (Cole), while the seeds contain 5-methylsulfinylpentyl, 5-methylthiopentyl, 4-pentenyl, and 2-hydroxy-4-pentenyl glucosinolates (Daxenbichler *et al.,* Kjaer). The remaining species of *Berteroa* have not been surveyed for fatty acids or glucosinolates.

Seed-coat anatomy of *Berteroa incana* is indistinguishable from that of *B. obliqua.* The epidermis in both has large columns with markedly flattened tops and hollow centers, while the palisade layer has isodiametric cells with strongly thickened radial and inner tangential walls (Vaughan & Whitehouse).

Except for the weedy *Berteroa incana* and *B. mutabilis,* the genus has very little economic importance. The leaves of *Berteroa* are said to be eaten as a salad (Crisp).

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24. **Draba** Linnaeus, Sp. Pl. **2**: 642. 1753; Gen. Pl. ed. 5. 291. 1754.

Annual, biennial, or most commonly perennial herbs, usually with much-branched caudices. Stems simple or branched, scapose or foliose. Trichomes simple, furcate, cruciform [malpighiaceous, pectinate, stellate, or dendritically branched], usually more than one kind present. Basal leaves petiolate or rarely sessile, entire or toothed to laciniate [rarely pinnately lobed], usually forming distinct rosettes in the perennials but rarely so in the annuals. Cauline leaves (when present) sessile [or petiolate], cuneate [or amplexicaul]. Inflorescences ebracteate [or bracteate], few- to many-flowered, corymbose racemes, slightly to greatly elongated in fruit; fruiting pedicels ascending to divaricate [or erect]. Sepals erect to spreading, oblong to elliptic or ovate, not saccate or only slightly so at base, usually membranaceous at margin, caducous [or persistent], glabrous or pubescent. Petals present, reduced or absent in some autogamous annuals, white [yellow, rarely lilac, violet, orange, or red], obovate to spatulate [orbicular or linear], obscurely to distinctly clawed, the apex obtuse or rounded to truncate, or shallowly to deeply emarginate, or bifid. Nectar glands tooth- or ringlike, usually subtending the bases of filaments, median glands sometimes absent. Stamens 6 [very rarely 4], usually tetradynamous; filaments free, unappendaged, linear, slender or sometimes dilated at base; anthers oblong to ovate, polliniferous [or pollen aborted or absent in agamospermous taxa]. Ovary glabrous or pubescent, [2-] to 80-ovulate. Fruits dehiscent, ovate, lanceolate, elliptic, oblong, linear [or orbicular], sessile, flat or spirally twisted, flattened parallel to the septum, sometimes slightly inflated; valves glabrous or pubescent, usually with a distinct midnerve and with obscurely to prominently anastomosing lateral nerves; septum membranaceous, complete, usually not veined; styles persistent, long to short or obsolete; stigmas capitate, entire or 2-lobed. Seeds [1–] 3–40 per locule, ovate to ellipsoid [or orbicular], usually flattened, light to dark brown, reticulate, nonmucilaginous when wet, wingless [or very rarely broadly winged], weakly to strongly biseriately arranged in each locule, pendulous on slender funicles; cotyledons accumbent. Base chromosome numbers 6–12. (Including *Abdra* Greene, *Aizodraba* Fourr., *Dolichostylis* Turcz., *Drabella* Fourr., *Drabella* Nábělek, *Erophila* DC., *Holargidium* Turcz., *Leptonema* W. J. Hooker, *Nesodraba* Greene, *Odontocyclus* Turcz., *Pseudobraya* Korsh., *Stenonema* W. J. Hooker, *Thylacodraba* O. E. Schulz, *Tomostima* Raf.) LECTOTYPE SPECIES: *D. incana* L.; see M. L. Green, Bull. Misc. Inf. Kew **1925:** 51. 1925. Britton & Brown (Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 148. 1913) chose *D. verna* L. as the lectotype species of *Draba.* This species, however, is the conserved type of *Erophila.* (Name from Greek *drabe,* acrid, used by Dioscorides to describe the taste of the leaves of certain cruciferous plants thought by some authors to have been hoary cress, *Cardaria Draba* (L.) Desv.) —WHITLOW GRASS.

A natural genus and the largest of the Cruciferae, with some 350 species distributed primarily in the Northern Hemisphere, particularly in the arctic and subarctic regions, as well as in the alpine and mountainous portions of the temperate regions. There are about 65 species in South America distributed at higher elevations from Colombia and Venezuela southward along the Andes into Patagonia. *Draba* is poorly represented in Mexico and Central America (11 species, six endemic; Rollins, 1984) and in Africa (five species, two endemic; Atlas Mountains of Morocco and Algeria) and is absent in Australia. More than 100 species are found in North America and Greenland, and the ranges of about 20 of these extend into the arctic and subarctic regions of Europe and/or Asia. The genus is well developed in the Himalayan and Irano-Turanian regions (ca. 50 and 40 species, respectively), as well as in China and Japan (ca. 35 species), Siberia and central Asia (ca. 30 species), central and northern Europe (ca. 35 species), and the Mediterranean area (18 species). *Draba* is represented in the southeastern United States by seven species, one of which is naturalized.

The sectional classification of *Draba* is controversial. Schulz (1927, 1936), who treated the genus on a worldwide basis, recognized 17 sections, while Tolmachev (1939) assigned the 91 species occurring in the U.S.S.R. to 29 series without recognizing sections. Although some of the infrageneric groups recognized by these authors represent natural assemblages of closely related species, the boundaries between the majority of them are artificially drawn and clearly unsatisfactory. Fernald (1934), who was the first to point out weaknesses in Schulz's (1927) sectional classification, indicated that his keys to the sections and to the species are misleading and impractical. It is beyond the scope of this flora to present a comprehensive sectional treatment for *Draba*. The genus is poorly represented in our area, and I prefer not to recognize any sections here.

Draba brachycarpa Nutt. (*Abdra brachycarpa* (Nutt.) Greene), $2n = 16, 24$, is the most widely distributed species in the Southeast. It grows on open clay soil in lawns, pastures, fields, disturbed areas, waste grounds, and cedar glades, on limestone rubble, and along roadsides in all of the Southeastern States. It appears to have restricted distribution in portions of the Florida Panhandle (Leon, Gadsden, Liberty, and Jackson counties) and in northern Louisiana. Its range extends west into Texas, north into Kansas, and east into Missouri, Illinois, Ohio, and Virginia. It is adventive in some of the Mountain and Pacific states. *Draba brachycarpa* is easily distinguished from the other annual drabas in our area by its glabrous, elliptic to oblong-lanceolate fruits 2–6 mm long, and by its cruciform, sessile trichomes. Diploid and triploid populations based on $x = 8$ have been found in Arkansas (Smith, 1969) and Texas (Rollins & Rüdenberg), respectively.

Draba aprica Beadle (*D. brachycarpa* var. *fastigiata* Nutt. ex Torrey & Gray) is a very close relative of *D. brachycarpa*. It grows on granite outcrops and in shallow sandy soils over siliceous rock. It is locally common in open knolls, woods, and alluvial areas near streams in South Carolina (Lancaster County), Georgia (Piedmont; Towns, Richmond, Oglethorpe, Cobb, and De Kalb counties), Arkansas (Drew, Faulkner, Cleburne, Washington, Montgomery, and Polk counties), eastern Oklahoma (McCurtain and Cherokee counties), and southeastern Missouri (Madison and Iron counties). Hitchcock suggested that *D. aprica* should be regarded as a variety of *D. brachycarpa*, but Fernald (1934) and Rollins (1961) clearly demonstrated that they are sufficiently different to be treated as distinct species. They do not hybridize in areas of sympatry, and according to Kral, *D. brachycarpa* flowers early and is usually in full fruit when plants of *D. aprica* start to bloom. Both species are white-flowered annuals with cruciform trichomes and small fruits to 6 mm long. *Draba aprica* differs from *D. brachycarpa* in its pubescent fruits, stalked trichomes, larger seeds (1–1.2 mm instead of 0.5–0.8 mm long), and corymbiform lateral branches of the infructescence (FIGURE 2g, j).

Draba ramosissima Desv. (*Alyssum dentatum* Nutt., *D. dentata* (Nutt.) W. J. Hooker & Arnott, *D. ramosissima* var. *glabrifolia* E. L. Braun), $2n = 16$, is a mat-forming perennial with much-branched, long caudices covered with remnants of old leaves and terminated by rosettes of laciniate to subpectinate leaves. It differs from its relatives with spirally twisted fruits in its paniculate infructescences with strongly divergent branches and in its styles 1–3 mm long. *Draba ramosissima* grows primarily on open shale banks, dolomitic bluffs, and limestone cliffs in North Carolina (Madison and Buncombe counties), Tennessee (Blount and Cocke counties), Kentucky, West Virginia, Virginia, and Maryland. Gattinger reported it from Polk County, Tennessee, but subsequent botanists have not confirmed this record. Plants with glabrous to sparsely pubescent stems and leaves were recognized by Fernald (1934, 1950) as var. *glabrifolia*. As shown by both Nye (1961, 1969a) and Reed, however, trichome

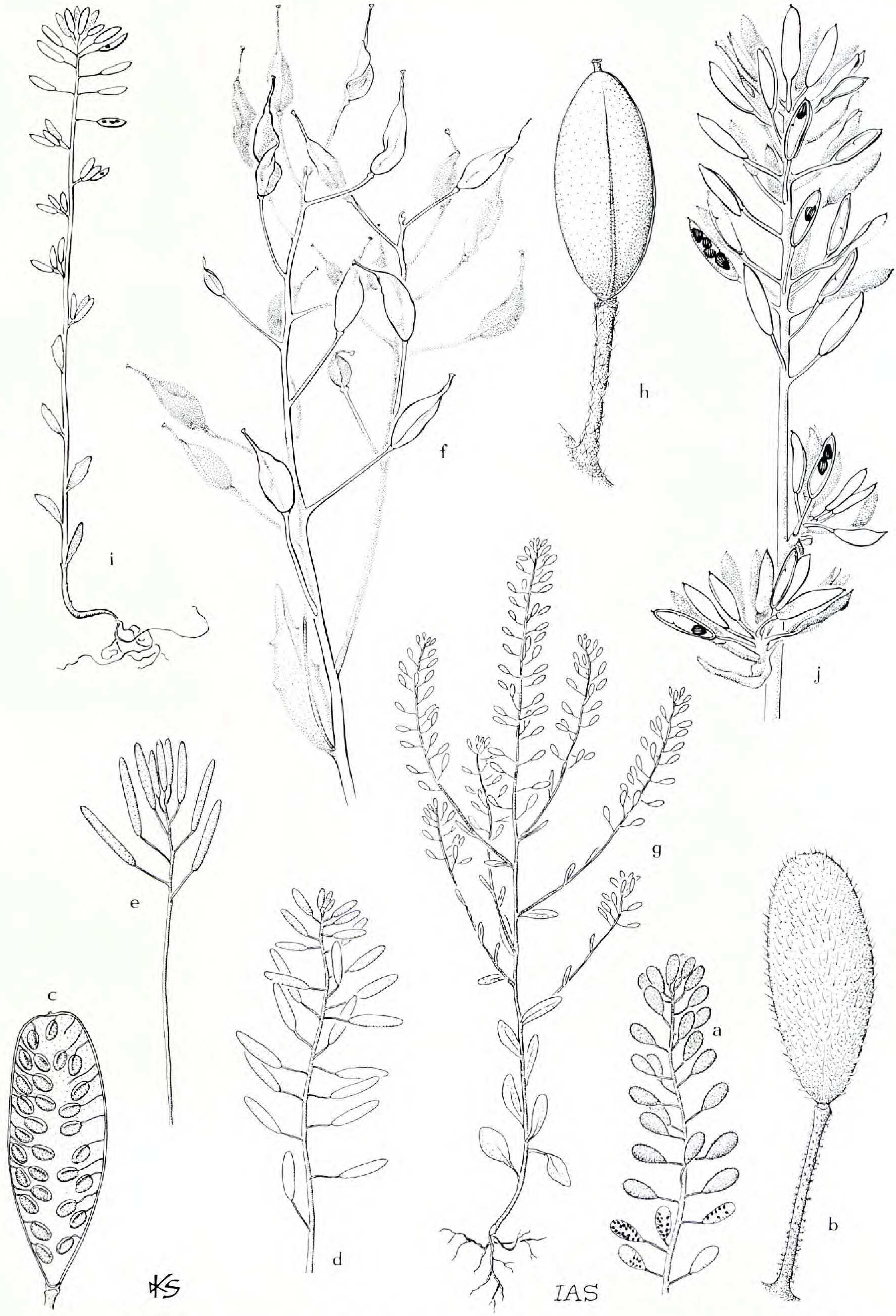

FIGURE 2. Selected species of *Draba*. a–c, *D. platycarpa:* a, infructescence, × ¾; b, fruit, × 5; c, fruit with 1 valve removed, × 5. d, *D. cuneifolia,* infructescence, × ¾. e, *D. reptans,* infructescence, × ¾. f, *D. ramosissima,* infructescence, × 2. g, h, *D. brachycarpa:* g, fruiting plant, × 1; h, fruit, × 12. i, j, *D. aprica:* i, fruiting plant, × 1; j, infructescence, × 2.

density is highly variable in the species, and both glabrous and pubescent forms are found within a given population. Schulz (1927) placed *D. ramosissima* in sect. PHYLLODRABA O. E. Schulz and assigned its nearest relative, *D. arabisans* Michx. (Maine to Newfoundland and westward to Minnesota and Ontario) to sect. LEUCODRABA DC. He separated these sections mainly on the basis of the many-leaved stems and yellow flowers in the former vs. the few-leaved stems and white flowers in the latter. Neither set of characters, however, was carefully observed or evaluated in either of the species or in the sections to which they were assigned.

The remaining species of *Draba* indigenous to the Southeastern States are very closely related. They were placed by Schulz (1927) in sect. TOMOSTIMA (Raf.) O. E. Schulz, which also included the South American *D. araboides* Wedd. and *D. australis* R. Br. All are subscapose annuals with subsessile basal leaves, obsolete styles, and heteromorphic flowers (some with broad, white petals, others apetalous and cleistogamous). *Draba reptans* (Lam.) Fern. (*Arabis reptans* Lam., *D. caroliniana* Walter, *D. micrantha* Nutt., *D. coloradensis* Rydb., *D. reptans* var. *stellifera* (O. E. Schulz) C. L. Hitchc.; see Hitchcock and Fernald (1934) for 15 additional synonyms), $2n = 16, 30, 32$, grows in open sandy areas, rock crevices, pastures, prairies, and disturbed sites, as well as along roadsides and railroad tracks. It is distributed from Massachusetts southward into North Carolina (Lincoln County), South Carolina (Darlington County), Georgia (Kenesau Mtn.), Tennessee (Nashville Basin), Alabama (Lee and Montgomery counties), Arkansas (Washington and Sebastian counties), and westward into the Pacific States, as well as in Manitoba, Ontario, and Saskatchewan. *Draba reptans* is easily distinguished from its nearest relatives by its entire or subentire leaves with simple or sometimes forked trichomes on the upper surface and stellate ones on the lower, and by its subumbellate infructescences with glabrous rachises and pedicels. Smith (1965) reported $2n = 16$ from plants of Kansas, but Löve & Löve found tetraploid populations ($2n = 32$) in Manitoba, and Mulligan (1966) counted $n = 15$ in plants from Saskatchewan and South Dakota.

Draba cuneifolia Nutt. ex Torrey & Gray is a variable and widely distributed species in which Hartman and colleagues recognized three varieties. Variety *cuneifolia* (*D. Helleri* Small, *D. ammophila* Heller, *D. cuneifolia* var. *leiocarpa* O. E. Schulz, *D. cuneifolia* var. *Helleri* (Small) O. E. Schulz, *D. cuneifolia* var. *foliosa* Mohlenbrock & Voigt), $2n = 32$, is widely distributed in northern and southern Arkansas, southeastern Kansas, Missouri, Oklahoma, the Southwestern States, central and western Colorado, western Utah, southern Nevada, and adjacent southeastern California. It is sporadic and probably introduced in North Carolina (New Hanover County), Florida (Duval, St. Johns, and Jackson counties), Alabama (Sumter County), Tennessee (Decatur County), Mississippi (Oktebbeha County), Louisiana (Grant, Rapides, and Caddo parishes), and Ohio. It is indigenous but apparently uncommon in Chihuahua, Coahuila, Baja California, and Zacatecas, Mexico. Mohr stated that *D. cuneifolia* is found in Georgia, but I have not seen any specimens from this state, and Hartman and colleagues did not list it from there. The species grows on limestone ledges, rocky slopes, and disturbed sandy soils in prairie pastures, lawns, grassy plains, fallow fields, cedar glades, and waste places. The other varieties of *D. cuneifolia,* var. *integrifolia* S. Watson and var. *sonorae* (Greene) S. B. Parish, do not occur in our area and are primarily distributed in the southern parts of California, Nevada, Arizona, and Texas and in adjacent northern Mexico. They differ from var. *cuneifolia* in their fruits with stellate instead of simple trichomes. Variety *cuneifolia* sometimes has glabrous fruits.

Draba platycarpa Torrey & Gray (*D. cuneifolia* var. *platycarpa* (Torrey & Gray) S. Watson, *D. viperensis* St. John), $2n$ = ca. 16, 32, differs from *D. cuneifolia* in its obovate to broadly elliptic, rounded fruits 2.5–3.7 mm wide and in its scapes pubescent with a mixture of long, simple trichomes and short, branched ones. The latter species has oblong to lanceolate or narrowly elliptic, acute fruits 1.8–2.8 mm wide and scapes with short, branched trichomes only. *Draba platycarpa* is sporadic in Louisiana (Lincoln Parish), Arkansas (Hempstead and Garland counties), and Oklahoma but is widespread in Texas and central and southern Arizona. It is disjunct and probably introduced in Idaho, Oregon, and Washington. Several authors (e.g., Watson, Hitchcock) reduced *D. platycarpa* to a variety of *D. cuneifolia,* but Hartman and colleagues have clearly shown that they should be treated as closely related species. They are morphologically distinct, and their profiles of flavonoid glucosides and volatile components are very different. They do not hybridize in areas of sympatry, and despite the numerous attempts to make artificial crosses between the two species, no hybrids were obtained (Hartman *et al.*). Diploid and tetraploid populations of *D. platycarpa* were found in Texas in Tarrant (Hartman *et al.*) and Kinney (Rollins & Rüdenberg) counties, respectively.

Draba verna L. (*Erophila verna* (L.) Chev., *E. vulgaris* DC.; see Schulz (1927) for more than 200 additional synonyms listed as species, varieties, or forms), whitlow grass, whitlow wort, $2n = 14, 16, 24, 30, 32, 34, 36, 38, 40, 52, 54, 58, 60, 64$, is a Eurasian plant naturalized throughout the New World. It has been reported from all of the Southeastern States except Louisiana and Florida. It is one of the earliest annuals to bloom in late winter and early spring (the generic name *Erophila,* under which *D. verna* is often placed, is derived from Greek *er,* spring, and *phileo,* to love, referring to its early appearance in spring). The species grows in lawns, fields, waste places, pastures, cedar glades, and open rangeland, on grassy hillsides, and along roadsides. It was well established in North America as early as the first half of the eighteenth century (Benson).

Draba verna is a highly variable and taxonomically difficult complex in which numerous extremes have been recognized as species, subspecies, or varieties. It consists of self-pollinating, morphologically distinct, uniform, local populations with different chromosome numbers. Crosses between such populations often produce hybrids that are sterile because of meiotic abnormalities. Autogamy played a major role in the formation and stabilization of a very large number of easily separable populations. Nearly 200 such populations were recognized by the nineteenth-century French botanist Alex Jordan as distinct "species," sometimes called "Jordanons." Schulz (1927) reduced these to eight species and some 60 varieties, but subsequent workers (e.g., Winge, 1940) questioned the taxonomic status of most of them. There is no correlation between the morphological, cytological, genetic, geographic, and ecological data on this complex, which is best recognized as a single polymorphic species with several subspecies. No attempt is made here to determine the subspecies of *D. verna* naturalized in the Southeastern United States.

Draba is a well-defined genus easily recognized by its latiseptate (flattened parallel to the septum), ovate to orbicular or oblong to linear fruits, usually wingless seeds biseriately arranged in each locule, unappendaged staminal filaments, accumbent cotyledons, and usually branched trichomes. The limits of the genus have not been altered during the past two centuries, and only one of its segregates is controversial. *Erophila,* which is united with *Draba* by North American botanists and retained as an independent genus by those elsewhere, differs from *Draba* only in its bifid instead of entire to deeply emarginate petals. The two are indistinguishable in every other morphological character. In my opinion this difference is not important; certain genera of the Cruciferae (e.g., *Megacarpaea* DC. and *Alyssoides*) have species with either entire or bifid petals. Petal apex (bifid vs. entire) may be controlled by a few genes or by a single pleiotropic gene and could therefore be insignificant for generic delimitations within the Cruciferae.

Perhaps the major taxonomic complexity in *Draba,* other than its sectional classification, lies in its species limits. Rollins (1966) suggested that apomixis together with polyploidy and interspecific hybridization are responsible for this complexity. Many species have been described on the basis of minor differences in characters of which the variation was poorly understood. For example, presence vs. absence of trichomes on fruits is insignificant in certain complexes, and numerous species (e.g., *D. reptans* and *D. cuneifolia*) have plants with either glabrous or pubescent fruits within the same population. On the other hand, the type of trichome (simple, furcate, cruciform, stellate, or dendritic) is very important in separating species.

Self-compatibility is apparently very common in *Draba,* and only a few species are self-incompatible (Bateman; Mulligan, 1976; Mulligan & Findlay). Protogyny occurs in a few species such as *D. aizoides* L. and *D. alpina* L. (Al-Shehbaz, 1977; Kay & Harrison), while autogamy is widespread in the genus. Species such as *D. reptans, D. cuneifolia,* and *D. aprica* produce heteromorphic flowers: some have sizeable petals, others have reduced ones, and still others are apetalous and cleistogamous (Fernald, 1934). They apparently produce apetalous flowers toward the end of the growing season (Kral), but *D. tenerrima* O. E. Schulz (Kashmir, Pakistan) is always apetalous and has only four stamens. Agamospermy occurs in the North American *D. densifolia* Nutt. ex Torrey & Gray, *D. Paysonii* Macbr., *D. ventosa* A. Gray, *D. exunguiculata* (O. E. Schulz) C. L. Hitchc., *D. Grayana* (Rydb.) C. L. Hitchc., *D. oligosperma* W. J. Hooker, and *D. streptobrachia* R. A. Price (Mulligan, 1976; Mulligan & Findlay; Price, 1979, 1980). In these species pollen fertility is zero or nearly so and the anthers do not dehisce. Some apomicts are triploids with highly irregular meiosis, but all produce abundant viable seeds without the need for pollen stimulation of seed production. Earlier claims of apomixis in *D. verna* (see Lotsy) were based on misinterpreted observations.

Chromosome numbers are known for some 115 species, the majority of which (nearly 60 percent) are polyploid; only a few (about 5 percent) have diploid and polyploid populations. Although base chromosome numbers in *Draba* range from six to 12, those of nearly 85 percent of the species are based on eight. Mulligan (1966) suggested that the North American species probably evolved through aneuploidy at the polyploid level. The lowest chromosome number in the genus ($2n = 12$) is found in *D. Olgae* Regel & Schmalh. (central Asia), while the highest counts ($2n = 128, 144$) are found in the North American *D. corymbosa* R. Br. ex DC. (including *D. macrocarpa* J. M. F. Adams and *D. Bellii* T. Holm), which consists of 16- and 18-ploid populations based on $x = 8$ (Böcher, 1966; Mulligan, 1974a). As shown above, *D. verna* is the most cytologically complex species in the genus. It contains many chromosomal races ranging from diploid to octoploid, as well as intermediate aneuploid derivatives.

Böcher (1966) indicated that the majority of the alpine species are diploid while the arctic ones are polyploid. He speculated that the mountains south of the arctic areas are probably the centers of origin and that *Draba* may be polyphyletic. He observed that polyvalent formations are very rare in drabas with high ploidy levels and suggested that allopolyploidy may have played an important evolutionary role at the hexaploid and decaploid levels.

Despite claims by many authors (e.g., Ekman (1932b), Schulz (1927), Weingerl) that interspecific hybridization is widespread in *Draba,* very little experimental work supports this. Fernald (1934) suggested that most of the alleged interspecific hybrids represent variations within poorly circumscribed, polymorphic species, while Knaben seriously questioned the validity of several hybrids listed by Ekman (1932b). There are strong sterility barriers between pairs of many closely related species. Mulligan (1974b, 1975, 1976) showed that artificial hybridization between many sexual species produces offspring with zero or very low pollen fertility and with aborted fruits. He concluded that interspecific hybridization is very rare in nature. Some members of the *D. nivalis* Liljeblad group produce sterile natural interspecific hybrids. Viable seeds were obtained from a few successful artificial crosses, but the second-generation hybrids did not reach maturity (Mulligan, 1975).

The chemistry of *Draba* is poorly studied, and only a few species have been surveyed for secondary constituents. Isopropyl, 2-butyl, allyl, 3-butenyl, and benzyl glucosinolates are found in four unrelated species (Kjaer; Rodman & Chew; Hartman *et al.*). The fatty-acid content of only six species has been determined (Jart).

Roots of certain rock-dwelling, perennial species of *Draba* have peculiar secondary growth characterized by the formation of armed periderm, abundant soft tissue, and secondary xylem structurally resembling the primary. These anatomical specializations, which are believed to be adaptations to rocky habitats, are also found in genera outside the Cruciferae (Pirogov).

Many species of *Draba* are cultivated as rock-garden or wall plants (Irving). Very few are weeds or show weedy tendencies. The fruiting stalks and seeds of *D. nemorosa* L. are used in China and Japan as diuretics and are prescribed to treat coughs, dropsy, nausea, and pleurisy (Perry; Kung & Huang). *Draba verna* (whitlow grass) was believed to cure whitlow, inflammation around the nails.

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25. **Lesquerella** S. Watson, Proc. Am. Acad. Arts Sci. **23:** 249. 1888.

Annual, biennial, or perennial herbs, usually densely pubescent with stellate [or lepidote] trichomes, sometimes pubescent with a mixture of simple, bifurcate, and dendritic ones. Stellate trichomes with few [to numerous] rays; rays smooth or tuberculate, simple or once [or twice] forked; webbing absent [or present only between the bases of rays, or progressively developed to their tips]. Stems decumbent to erect, several to numerous or rarely solitary, usually arising laterally from the basal rosette. Basal leaves petiolate, entire or dentate to sinuate or lyrately to pinnately lobed. Cauline leaves petiolate or sessile, usually cuneate at base, sometimes auriculate or amplexicaul, entire to dentate [rarely sinuate or incised]. Inflorescences ebracteate, few- to many-flowered, corymbose racemes; infructescences lax [or congested]; fruiting pedicels persistent, ascending to horizontal [or reflexed], straight or curved [sometimes sigmoid]. Sepals pubescent, narrowly oblong or elliptic to broadly ovate [occasionally linear or obovate], ascending to spreading [or erect], almost always deciduous, green or yellowish; lateral pair usually saccate, median pair not saccate, often thickened and somewhat cucullate at apex. Petals yellow to orange, sometimes white or lavender and with [or without] a yellow center [or purple veins], glabrous, broadly obovate [to narrowly spatulate], undifferentiated or slightly differentiated into claw and blade, obtuse or retuse to emarginate at apex. Nectar glands usually forming a ring [or a hexagon] subtending the bases of median filaments and surrounding those of lateral stamens. Stamens 6, tetradynamous; filaments linear, unappendaged, not dilated or sometimes strongly dilated at base; anthers linear [to oblong or ovate], usually sagittate at base. Fruits globose to subdidymous, sometimes obovoid to subpyriform [or ovoid to oblong], inflated or rarely strongly flattened parallel [or at right angles] to the septum, sessile or stipitate; valves glabrous or variously pubescent on the exterior or on both outer and inner surfaces, obscurely or rarely strongly nerved, thick or sometimes papery or membranaceous, rounded [or rarely strongly keeled] on the back; replum glabrous or pubescent; septum complete or occasionally with a central perforation, rarely reduced to a narrow band around the inner margin of replum, usually with a conspicuous nerve extending from the base of style to about or slightly beyond the middle, translucent or opaque; styles slender, persistent, glabrous or pubescent; stigmas capitate, entire or slightly 2-lobed, often much greater in diameter than the tip of style; ovules 2–14[–20] per locule; base of funicles usually adnate to septum. Seeds reticulate, orbicular or suborbicular, rarely hemispherical [or oblong to oval], flattened or rarely plump, with or without a narrow margin or wing, nonmucilaginous [or copiously mucilaginous] when wet; cotyledons accumbent [or rarely obliquely accumbent], longer [or equaling to shorter] than the radicle. Base chromosome numbers 5–10. LECTOTYPE SPECIES: *L. occidentalis* (S. Watson) S. Watson; see Payson, Ann. Missouri Bot. Gard. **8:** 133. 1922. The arbitrary designation of *L. Lescurii* (A. Gray) S. Watson as the lectotype species of the genus by Britton & Brown should be rejected because it is in conflict with Watson's original description of *Lesquerella.* For further discussion on the subject, see Payson and Rollins & Shaw (1973). (Name honoring Charles Leo Lesquereux, Nov. 18, 1806–Oct. 25, 1889, a distinguished Swiss-born, American paleobotanist and bryologist.)—BLADDERPOD.

A well-defined genus of some 90 species, the majority of which (83 species and 27 infraspecific taxa) occur in North America, particularly in the southwestern United States and adjacent Mexico, the Rocky Mountains, and the intermontane basin of the western United States. The remainder (probably up to 12 species; Rollins & Shaw, 1973) are found in South America from Bolivia southward. One species, *Lesquerella arctica* (Wormsk. ex Hornem.) S. Watson, is widely distributed from the coasts of Greenland across the Canadian Arctic and Alaska into Siberia. The genus is represented in the southeastern United States by seven species, of which five are endemic.

The sectional classification of *Lesquerella,* as proposed by Watson and Payson, does not reflect the natural groupings of species. The former recognized two sections: sect. ALYSMUS S. Watson (five species; plants not canescent, filaments dilated at base, cauline leaves usually auriculate) and sect. LESQUERELLA (28 species; plants canescent, filaments slender at base, cauline leaves not auriculate). Payson, on the other hand, redefined sect. ALYSMUS to include only one species, *L. Lescurii,* with latiseptate fruits (flattened parallel to the septum). He placed in sect. ENANTIOCARPA Payson three species said to have angustiseptate fruits (flattened at right angles to the septum) and retained in sect. LESQUERELLA (as sect. *Eulesquerella*) the remaining 48 species, with inflated, globose or ovoid fruits. On the basis of chromosome numbers, fatty-acid content, cross-fertility, and several morphological features, *L. Lescurii* is very closely related to several species with globose fruits. Therefore, sect. ALYSMUS is clearly artificial. One of the three species assigned by Payson to sect. ENANTIOCARPA is a *Draba,* while the other two are definitely unrelated (Rollins & Shaw, 1973). Slightly angustiseptate fruits probably evolved independently a few times within *Lesquerella,* and alone they can be unreliable indicators of relationships. As indicated by Rollins & Shaw (1973), the sectional classification of *Lesquerella* was not based on well-founded facts. It is impractical to place a few species in one or two sections and to retain the bulk of a genus in a highly heterogeneous one.

Lesquerella gracilis (W. J. Hooker) S. Watson (*Vesicaria gracilis* W. J. Hooker, *Alyssum gracile* (W. J. Hooker) Kuntze, *V. polyantha* Schlecht., *L. polyantha* (Schlecht.) Small), cloth-of-gold, $2n = 12$, is represented in the Southeastern States by subsp. *gracilis.* It grows on sandy loam or alkaline soil in prairies, pastures, and old fields, as well as along roadsides and grassy banks, in Arkansas (Howard and Little River counties), eastern Mississippi (Chickasaw, Lee, and Lowndes counties), southern Oklahoma, and east-central Texas. It is weedy and has been introduced in Tennessee in Shelby and Davidson counties (Rogers & Bowers) and in Missouri and Illinois. The subspecies is distinguished by its stipitate, glabrous, globose or ellipsoid fruits 3–6 mm long; cuneate, sessile or short-petiolate cauline leaves; 4–10(–14) ovules per locule; stellate trichomes with 4–7 bilaterally oriented rays; and straight, usually divaricate fruiting pedicels.

The records of *Lesquerella gracilis* subsp. *Nuttallii* (Torrey & Gray) Rollins & E. Shaw from Arkansas by Small (1913) (as *L. Nuttallii* Torrey & Gray and *L. repanda* (Nutt.) S. Watson) and by Payson (as *L. gracilis* var. *repanda* (Nutt.) Payson) were shown by Rollins & Shaw (1973) to be based on plants from Texas and Oklahoma, respectively. Subspecies *Nuttallii* differs from subsp. *gracilis* in its obpyriform to narrowly obovoid fruits (4.5–)5.5–9 mm long with a truncate base, instead of globose or ellipsoid fruits 3–6 mm long with a rounded base. Small (1913, p. 471) also indicated that *L. angustifolia* (Nutt.) S. Watson occurs "on prairies, near the Red River, Arkansas," but the record was from Red River County, Texas.

Lesquerella globosa (Desv.) S. Watson (*Vesicaria globosa* Desv., *V. Shortii* Torrey & Gray, *Alyssum globosum* (Desv.) Kuntze, *A. Shortii* (Torrey & Gray) Kuntze), $2n = 14$, has no close relatives in the genus and is clearly unrelated to any of the six species occurring in the Southeast. It is distributed in central Tennessee (Maury, Davidson, Cheatham, and Montgomery counties), north-central Kentucky, and Indiana (Posey County). The species was said to occur in Benton and Franklin counties, Arkansas (Smith), but I have not seen any material from this state, and neither Rollins & Shaw (1973) nor Kral has indicated that it is found there. It is most common on open rocky areas, limestone ledges, and cliffs along rivers but also grows in cedar glades and pastures and on open talus slopes. *Lesquerella globosa* has numerous small, globose, pubescent fruits (1–)2–2.8 mm long with a conspicuously wrinkled septum (FIGURE 3b); usually one subhemispherical seed per locule; straight fruiting pedicels; sessile or short-petiolate cauline leaves; and stellate trichomes with three to six usually forked rays.

The five remaining species of *Lesquerella* are endemic to the Southeastern States. All are annuals with a mixture of simple and branched (but never stellate) trichomes, auriculate cauline leaves, and staminal filaments with strongly dilated bases. They are diploids ($2n = 16$) that produce fully fertile offspring when hybridized (see below) in any combination. Furthermore, they contain high concentrations of densipolic acid, a unique seed fatty acid. The morphological, geographic, cytological, chemical, and interfertility data clearly support the derivation of the five species from a common ancestor.

Lesquerella lyrata Rollins, $2n = 16$, is a narrow endemic that grows in open pastures, old fields, cedar glades, and bottom lands, on limestone hills, and along roadsides in Franklin and Colbert counties, Alabama (Webb & Kral). Although it is locally common in a few localities, it is an endangered species. *Lesquerella lyrata* is readily distinguished from the other auriculate-leaved species by its yellow flowers and its glabrous, depressed-globose fruits with an opaque, complete septum and thick, leathery valves.

Lesquerella densipila Rollins, $2n = 16$, occurs in open alluvial sites, fallow fields, pastures, river bottoms, roadbanks, and cedar glades. It is abundant in the Central Basin of Tennessee, particularly near the West Fork of Stones

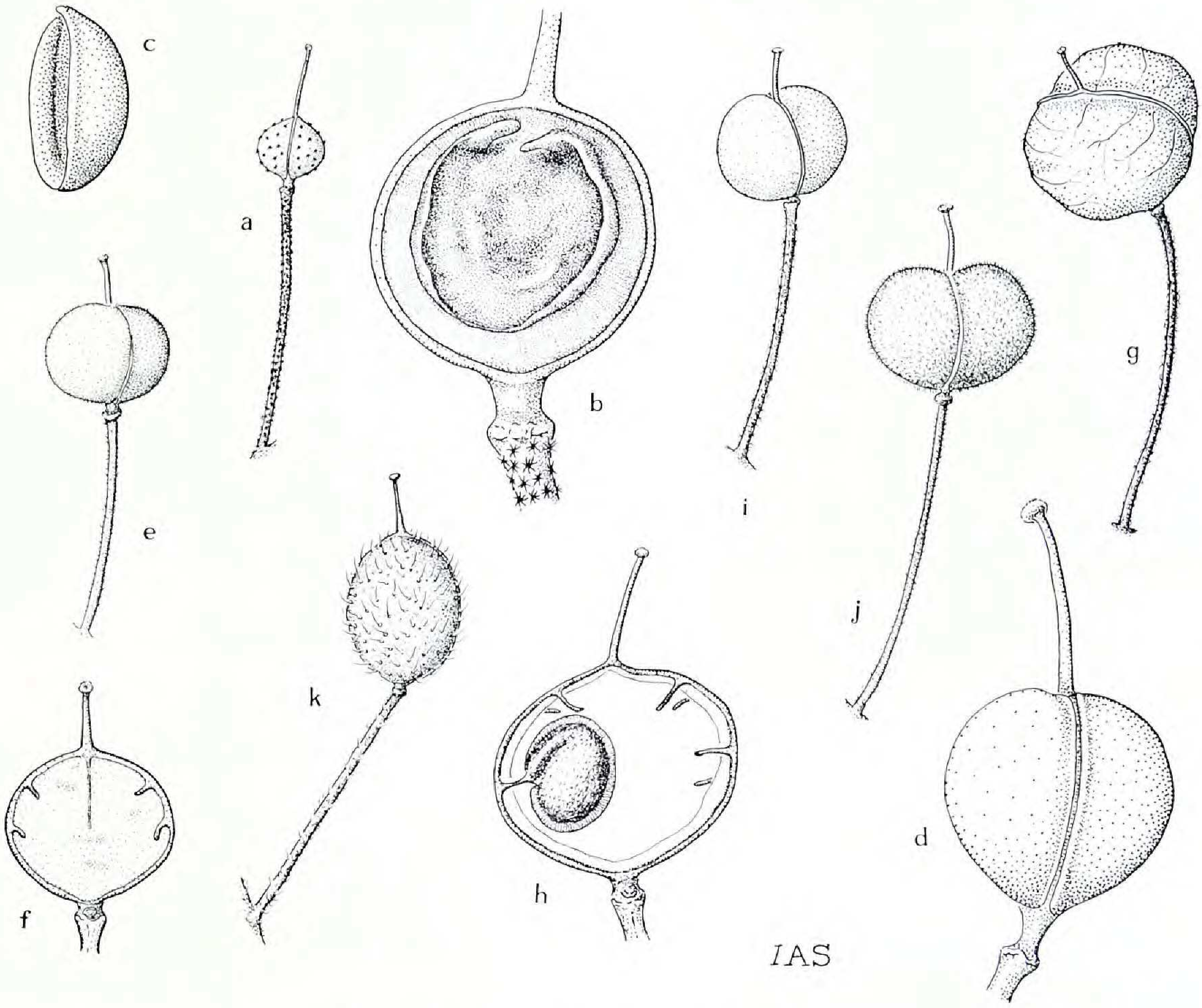

FIGURE 3. Fruits of *Lesquerella*. a–c, *L. globosa:* a, fruit, × 3; b, septum and replum, × 12—note wrinkled septum and position of seed; c, hemispherical seed, × 12. d, *L. gracilis,* fruit, × 5. e, f, *L. densipila:* e, fruit, × 3½; f, replum and septum, × 5—note midvein. g, h, *L. perforata:* g, fruit, × 2½; h, septum and replum, × 5—note central perforation. i, *L. lyrata,* fruit, × 3. j, *L. stonensis,* fruit, × 2½. k, *L. Lescurii,* fruit, × 3.

River, the Duck River, and the upper Harpeth River (Rutherford, Bedford, Williamson, Marshall, Maury, and Davidson counties). It also occurs, probably as a recent introduction, in northern Alabama (Franklin, Lawrence, Morgan, and Marshall counties). *Lesquerella densipila* is a very close relative of *L. lyrata,* from which it can be distinguished by its dense indumentum of short, simple or branched trichomes on the styles and the outer valve surfaces. According to Rollins (1955), *L. lyrata* is morphologically and geographically intermediate between *L. densipila* and *L. auriculata* (Engelm. & Gray) S. Watson (central Texas and south-central Oklahoma) and may well be the evolutionary link between the latter species and the auriculate-leaved members endemic to Tennessee.

On the basis of fruit morphology, earlier authors considered *Lesquerella Lescurii* (A. Gray) S. Watson (*Vesicaria Lescurii* A. Gray, *Alyssum Lescurii* (A. Gray) A. Gray), $2n = 16$, to be anomalous in the genus, and Payson placed it in a monotypic section. As shown above, however, the species is very closely related to and readily hybridizes with the auriculate-leaved lesquerellas of the Southeast. It is most closely related to and was probably derived from *L. densipila. Lesquerella Lescurii* is readily distinguished from all other species of the genus by its fruits that are strongly flattened parallel to the septum and its valves that are pubescent with a mixture of long, simple, bulbous-based trichomes and short, branched ones. It grows in open areas of river-bottom pastures, fields, and flood plains, as well as on thin soil over limestone in cedar glades and on hill slopes, in north-central Tennessee (Summer, Wilson, Rutherford, Davidson, Williamson, Cheatham, Montgomery, Dickson, and Stewart counties), particularly along the Cumberland River and several tributaries of the Harpeth River. Rollins (1981) listed *L. Lescurii* as having weedy tendencies. It is adventive and has been recorded only recently from Alabama (Limestone County) and Kentucky (Trigg County), by Kral and Chester, respectively.

A narrow endemic of central Tennessee, *Lesquerella stonensis* Rollins, $2n = 16$, grows in pastures, flood plains, and fields and on knoll tops, as well as on roadsides and stream banks along the East Fork of the Stones River (Rutherford County). According to Kral, it is locally abundant in some years and almost absent in others, with its present range restricted to a few fields along the Stones River.

Lesquerella perforata Rollins, $2n = 16$, is the nearest relative and perhaps a direct descendant of *L. stonensis.* It is also a narrow endemic of Tennessee and is presently known only within a radius of six miles around Lebanon (Wilson County), where it grows in open fields, pastures, floodplains, and limestone glades. Both species are easily distinguished from the other auriculate-leaved lesquerellas by their perforated septa (FIGURE 3h) and their white petals with yellow claws. *Lesquerella stonensis* has densely hirsute, depressed-globose to subdidymous fruits, hirsute styles, and glabrous inner-valve surfaces, while *L. perforata* has glabrous to sparsely hirsute, pyriform to obovoid fruits, glabrous styles, and densely pubescent inner-valve surfaces.

In no other genus of Cruciferae has natural interspecific hybridization been so well documented as in *Lesquerella.* In a series of papers, Rollins (1954, 1957) and Rollins & Solbrig (1973) demonstrated that species pairs involving *L. Lescurii, L. densipila,* and *L. stonensis* hybridize in all three combinations in parts of Tennessee where their ranges come together. Hybrid populations of *L. densipila* × *L. stonensis* (*L.* ×*maxima* Rollins, *L. densipila* var. *maxima* Rollins) were found in Rutherford and Davidson counties along the Stones River downstream from the junction of its East and West forks, where *L. stonensis* and *L. densipila,* respectively, grow. Those hybrids were more similar to the former than to the latter species. The hybrid *L. Lescurii* × *L. densipila* occupied a stretch of more than 40 miles downstream along the Harpeth River between its junctions with Arrington Creek and the Cumberland River in Williamson, Davidson, and Cheatham counties. The third hybrid combination, *L. stonensis* × *L. Lescurii,* was found only once (in a vacant lot in the town of La Vergne, Rutherford County) and was not directly associated with any river system, unlike the other hybrid combinations.

The establishment, persistence, and population size of hybrids or their parental species in a given area are influenced by spring flooding of rivers, agricultural practices, and factors controlling seed germination. For example, the hybrid *Lesquerella Lescurii* × *L. densipila,* which was estimated in 1955 to occupy approximately 600 acres around the junction of Arrington Creek and the Harpeth River (Rollins, 1957), was reduced to less than 10 plants in 1966 because of the conversion of that area into pasture land (Rollins & Solbrig, 1973). Man's agricultural activities in the Central Basin of Tennessee have played a major role in bringing the ranges of the auriculate-leaved species of *Lesquerella* into contact and consequent hybridization. These species are largely allopatric and presumably evolved and persisted in isolation from each other until a few decades ago. Very high degrees of interspecific fertility exist among *L. Lescurii, L. densipila, L. stonensis, L. perforata,* and *L. lyrata.* Artificial hybrids between any pair of these show very low levels of meiotic irregularities that are not significantly different from those observed within each parental species (Rollins, 1957; Rollins & Solbrig, 1973). The artificial first- and second-generation hybrids have very high pollen quality, and their seeds germinate at levels as high as 86 percent.

Many authors (e.g., Maguire & Holmgren; Mulligan; Payson; Rollins, 1939a, 1950, 1983; Rollins & Shaw, 1973) have emphasized the very close relationship between *Lesquerella* and *Physaria* (Nutt.) A. Gray (22 species; Alberta, the Pacific and Mountain states, Arizona, and New Mexico). It is generally agreed that *Physaria* is derived from *Lesquerella.* The line separating them is artificially drawn, and there is a continuous morphological gradation from one to the other. Both genera, however, should be maintained. Similar situations exist between pairs of related genera throughout the Cruciferae, and it is not practical to merge the larger *Lesquerella* with the smaller and earlier-published *Physaria* (Rollins, 1950; Rollins & Shaw, 1973). *Physaria* differs from *Lesquerella* in its highly inflated, always didymous fruits either markedly constricted at the replum or strongly flattened contrary to the septum (angustiseptate). In general, the fruits of *Lesquerella* are not inflated, not didymous, and not constricted at the replum. There are, however, some exceptions. In *L. inflata* Rollins & Shaw and *L. perforata* the fruits are inflated, while in *L. hemiphysaria* Maguire and *L. stonensis* they are subdidymous. Angustiseptate fruits are found in unrelated species of *Lesquerella* and are well developed in *L. carinata* Rollins, *L. Paysonii* Rollins, and *L. lasiocarpa* (W. J. Hooker) A. Gray var. *Berlandieri* (A. Gray) Payson. *Physaria oregona* S. Watson, *P. Geyeri* (W. J. Hooker) A. Gray, and *P. alpestris* Suksd. have slightly inflated fruits. They were transferred to *Lesquerella* by Mulligan but, as shown by Rollins & Shaw (1973), should be retained in *Physaria.*

Lesquerella is also related to *Synthlipsis* A. Gray (three species; Texas and northern Mexico), and *L. lasiocarpa* var. *Berlandieri* was suggested as the possible link between the two genera (Rollins, 1955; Rollins & Shaw, 1973). The Old World genera *Alyssoides* (= *Vesicaria* Adanson) (four species; southern France, Balkan peninsula, Turkey) and *Alyssum* were also said to be closely related to *Lesquerella* (Rollins, 1950; Rollins & Shaw, 1973). Both *Alyssum* and *Alyssoides* have stellate trichomes indistinguishable from those of *Lesquerella,* but they differ in their winged or appendiculate staminal filaments, their pollen morphology, their winged seeds, and their lack of a nerve in the septum. In my opinion, *Lesquerella* should be associated only loosely with *Alyssum* and *Alyssoides*.

The tribal disposition of *Lesquerella* is problematic. Schulz placed the genus in the tribe Drabeae and assigned its nearest relative, *Physaria,* to the tribe Lepidieae. He defined the latter tribe mainly on the basis of its angustiseptate fruits. As delimited by Rollins & Shaw (1973), however, *Lesquerella* contains several species (see above) with such fruits. According to Schulz's key to the tribes, various species of *Lesquerella* will be identified in the Alysseae, the Drabeae, and the Lepidieae. Angustiseptate fruits evolved independently in at least four tribes of the Cruciferae (Al-Shehbaz, 1986). Angustiseptate and latiseptate fruits are found in *Lesquerella, Graellsia* Boiss., *Smelowskia* C. A. Meyer, and *Nerisyrenia* Greene. Therefore, the type of flattening of fruits is not always useful for assigning genera to tribes. Rather, problematic genera such as *Lesquerella* should be placed in the tribe containing what seem to be their nearest relatives.

On the basis of pollen morphology, *Lesquerella* should be associated with *Physaria, Synthlipsis, Nerisyrenia,* and *Dimorphocarpa* Rollins. All these New World genera have 5- to 10-colpate pollen grains not found elsewhere in the Cruciferae (Rollins, 1979; Rollins & Banerjee, 1979; Rollins & Shaw, 1973). The last genus is closely related to *Dithyrea* Harvey, which has 4-colpate pollen. Because all of these genera have angustiseptate fruits and are traditionally assigned to the Lepidieae, there is no major obstacle to placing *Lesquerella* with them. Von Hayek's grouping of these genera in one tribe was more natural than Schulz's, but he assigned them, along with several unrelated genera, to the tribe Schizopetaleae Prantl, which was considered to have a polyphyletic origin from tribe Thelypodieae Prantl. In this paper I have placed *Lesquerella* in the Alysseae, following the modified tribal classification adopted earlier (Al-Shehbaz, 1984). It is obvious, however, that the genus is more appropriately placed with its nearest relatives in the Lepidieae.

Although individual flowers are not showy in *Lesquerella,* they are densely grouped in compact inflorescences that can be quite attractive. These are visited by various species of flies, butterflies, and solitary bees, but the most common pollinator in the Southeast is the introduced honey bee (*Apis mellifera*). Self-incompatibility is widespread in *Lesquerella* and occurs in all of the auriculate-leaved species growing in our area (Rollins, 1957; Rollins & Solbrig, 1973; Sampson).

Chromosome numbers have been reported for at least 52 species, the majority of which are diploid with $n = 5$ to 10. Polyploidy did not play a major role in the evolution of *Lesquerella,* and only ten species have both diploid and polyploid populations. Three species, *L. mendocina* (Phil.) Kurtz (South America), *L. arctica,* and *L. peninsularis* Wiggins (Baja California) are polyploid, with $2n = 50$, 60, and ca. 40 or 48, respectively. Diploid, tetraploid, and hexaploid populations are found in *L. Engelmannii* (A. Gray) S. Watson ($x = 6$) and *L. ludoviciana* (Nutt.) S. Watson ($x = 5$). Complex aneuploid series occur in both *L. argyraea* (A. Gray) S. Watson and *L. ovalifolia* Rydb. subsp. *ovalifolia* (Clark; Rollins & Shaw, 1973). Except for *L. grandiflora* (W. J. Hooker) A. Gray ($2n = 18$) and *L. lasiocarpa* ($2n = 14$), the remaining auriculate-leaved species have $2n = 16$. The uniformity in chromosome numbers and in the presence of densipolic acid (see below) support the placement of these auriculate-leaved species in a position somewhat remote from *L. grandiflora* and *L. lasiocarpa.*

Seeds of the auriculate-leaved species of *Lesquerella* endemic to the Southeast (*L. densipila, L. Lescurii, L. lyrata, L. perforata,* and *L. stonensis*) contain high concentrations of densipolic acid (C_{18}) and lack lesquerolic acid (C_{20}). Those of sixteen other species (including *L. grandiflora* and *L. lasiocarpa*) are rich in lesquerolic acid (45–72 percent of the total fatty-acid content). In *L. auriculata,* which is believed to be the link between the auriculate-leaved species of the Southeastern States and the rest of the genus, small amounts of densipolic (two percent) and lesquerolic (ten percent) acids were found, in addition to high concentrations (32 percent) of auricolic acid. The last is lacking in our auriculate-leaved species and is only a minor constituent in many other species of *Lesquerella* (Appelqvist). It is a higher homologue of densipolic acid, while lesquerolic acid is a higher homologue of ricinoleic acid, a trace acid present throughout the genus.

Five glucosinolates were found in 13 species (Daxenbichler *et al.,* 1961, 1962). 6-Methylthiohexylglucosinolate occurs in all of the auriculate-leaved species (*Lesquerella auriculata* was not analyzed) and in *L. Engelmannii.* Other compounds were 4-methylthiobutyl, 3-methylthiopropyl, isopropyl, and 2-butyl glucosinolates.

Trichome diversity in *Lesquerella* is probably greater than that in any other genus of Cruciferae. Rollins & Banerjee (1975, 1976) studied the trichomes of 69 species of *Lesquerella* and observed well-marked trends of specialization. From the dendritic type (stalked, with unequal branches forming an irregular pattern), which is presumably primitive, stellate trichomes evolved by the reduction of irregularities in branching and by the disposition of the rays in one plane. Further specialization from stellate trichomes with few, simple rays proceeded in two directions. The first trend, found in many species, is a progressive increase in the branching of rays. As a result, two- or four-forked rays either without thickened bases (*L. macrocarpa* A. Nelson) or with massively thickened and fused bases (*L. Hitchcockii* Munz, *L. rubicundula* Rollins, and *L. thamnophila* Rollins & Shaw) probably evolved. In the second trend, found in at least ten species, the increase in the number of simple rays is correlated with a centrifugal increase of webbing between the rays. The two representative extremes of this trend are *L. Douglasii* S. Watson (with about 13 rays webbed only between their bases) and the highly specialized *L. mexicana* Rollins (with ca. 50 rays webbed to their tips and forming peltate scales).

The trichomes of the Cruciferae are unicellular, and those of *Lesquerella* have calcium carbonate deposited as calcite on the interior of the cell wall (Lanning, 1961). Rollins & Shaw (1973) indicated that there is a broad correlation between the density of trichomes and the availability of moisture. Species growing in arid areas and at high elevations have the densest trichome covering, while those of mesic areas have a sparse indumentum. Ancíbor showed that the fully developed trichome remains alive and has a very conspicuous nucleus and a dense cytoplasm. She suggested that trichomes may have a waterabsorbing function, but Rollins & Shaw (1973) indicated that they probably reduce water loss from plants of arid areas by reflecting light rays, by forming a layer that slows down air movement, and by establishing a moisture gradient between the epidermis and the open air.

Lesquerella has little if any economic value. Several species analyzed for fatty-acid content show very high concentrations of hydroxy acids, which are valuable in industry. Tough plastics and reinforced elastomers have been produced from the oils of *L. Palmeri* S. Watson. Hinman (1984, 1986) suggested that *L. Fendleri* (A. Gray) S. Watson has superior qualities and can compete with castor bean (*Ricinus communis* L.) in its industrial oils. It has no allergenic or toxic properties, is capable of growing on sandy or calcareous soils of semiarid areas, tolerates cold and drought, and can be harvested by combine. No species of the genus, however, is a crop, and the agronomic values of most have not been evaluated.

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26. **Camelina** Crantz, Stirp. Austriac. **1:** 17. 1762.

Spring or winter annual or biennial herbs, with furcate-stellate and[/or] simple trichomes, sometimes glabrescent; stems simple or branched at base, often branched above. Basal leaves petiolate or subsessile, usually not in a rosette, entire to sinuate. Cauline leaves sessile, sagittate or amplexicaul, oblong to linear or lanceolate, entire or dentate, gradually decreasing in size upward. Inflorescences ebracteate, corymbose racemes, greatly elongated in fruit; fruiting pedicels horizontal to ascending [or appressed to rachis]; rachis of infructescence straight [or flexuous], glabrous [or pubescent]. Sepals oblong, erect, equal, not saccate at base, usually membranaceous at margin, villous in bud, often glabrescent. Petals yellow to white, clawed, spatulate, attenuate at base, longer than sepals. Nectar glands 4, 1 on each side of lateral stamens, median glands absent. Stamens 6, usually in 3 different lengths; filaments linear, free, unappendaged, slightly dilated at base; anthers oblong to ovate. Fruits usually dehiscent, obovate or narrowly to broadly pyriform [or linear], somewhat flattened parallel to the septum, short stipitate, strongly keeled and narrowly winged at the replum, rounded [truncate or notched] at apex, ending abruptly in a stylelike beak; valves thick, slightly to strongly convex, obscurely to prominently reticulate, the midvein evident in the lower half or along the entire length of the valve, glabrous [or pubescent], glossy on inside, the acuminate apex extending 0.5–1.5 mm into the beak area; beaks longer to shorter than styles; styles filiform, persistent; stigmas capitate; replum covered by the connate margins of valves, becoming visible after fruit dehiscence. Seeds 4–12 per locule, reticulate, oblong, copiously mucilaginous when wet, biseriately [or uniseriately] arranged in each locule; cotyledons incumbent or rarely accumbent. Base chromosome numbers 6, 7, 10, 13. (Including *Dorella* Bubani, non Weber–van Bosse, *Linostrophum* Schrank.) TYPE SPECIES: *Myagrum sativum* L. = *Camelina sativa* (L.) Crantz. (Name of obscure origin, possibly derived from Greek *chamai,* dwarf or on the ground, and *linon,* flax, perhaps referring to the stunting or suppressing influence of *Camelina* on the growth of flax.) —FALSE FLAX, GOLD-OF-PLEASURE, FLAXWEED.

A well-marked genus of six or seven species centered in Turkey and adjacent parts of southwestern Asia and southeastern Europe. *Camelina* is represented in North America by four naturalized species, of which two occur in the southeastern United States.

Of the two sections recognized in *Camelina* by De Candolle (1821, 1824), sect. CAMELINA (as sect. *Chamaelinum* DC.) is now retained in the genus, while sect. PSEUDOLINUM DC. has been transferred to *Rorippa* Scop. Boissier's sectional classification, which was accepted by Schulz and neglected by many subsequent authors, is more practical than any other infrageneric classification of *Camelina.* The monotypic sect. ERYSIMASTRUM Boiss. (fruits linear-cylindrical, seeds uniseriate) includes *C. anomala* Boiss. & Hausskn. of southern Turkey and the Bekaa valley, Lebanon. Section CAMELINA (fruits obovate to pyriform, seeds biseriate) contains the remaining species of the genus. On the basis of seed size and other characters of continuous nature, Mirek (1981) recognized two series in *Camelina.* It is doubtful, however, that these improve the taxonomy of the genus.

Camelina microcarpa Andrz. ex DC. (*C. sativa* subsp. *microcarpa* (Andrz.) E. Schmid), false flax, $2n = 40$, which is naturalized throughout North America, grows in grainfields, meadows, waste places, and disturbed habitats, as well as along roadsides, in North and South Carolina, Georgia, Tennessee, Arkansas, and Louisiana. It is likely to be found in the remaining states of the Southeast. It is distinguished by its mixed simple and furcate-stellate trichomes on the lower part of the stem, fruits 2.5–5 mm long, petals to 4.2 mm long, and seeds 0.9–1.5 mm long.

Most of the earlier reports of *Camelina sativa* (L.) Crantz (*Myagrum sativum* L., *Alyssum sativum* (L.) Scop., *C. sativa* var. *glabrata* DC., *C. glabrata* (DC.) K. Fritsch), false flax, flaxweed, gold-of-pleasure, Dutch-flax (Small), $2n = 40$, from North and South Carolina, Tennessee, Arkansas, and Louisiana are doubtful and may well represent misidentifications of plants of *C. microcarpa. Camelina sativa* is less common in North America than *C. microcarpa* and may be only a waif in the southeastern United States. It is distinguished from *C. microcarpa* by its glabrous or sparsely stellate-furcate stems rarely with simple trichomes, its longer fruits 7–9 mm long, and its shorter infructescences with fewer fruits.

Camelina Rumelica Velen., which has only recently been recorded in the United States (McGregor, 1984), is easily confused with *C. microcarpa* because of similarities in fruit shape and size, seed length, and lack of trichomes on the infructescence. It differs in its petals 5–9 mm long, in having only simple trichomes with some usually 2–3.5 mm long, and in its fruits more widely spaced in the lower than the upper part of the infructescence. The species is naturalized in Oklahoma, Texas, Kansas, Colorado, Nevada, and Oregon.

Camelina has obovate-pyriform (very rarely linear) fruits, thick valves abruptly acuminate into a stylelike beak (FIGURE 1e), and connate valve margins that make the replum invisible until dehiscence. The genus is related to *Chrysochamela* Boiss. (three species; Turkey and Syria) but certainly not to *Neslia* Desv., *Capsella* Medicus, or *Cochlearia* L., as has been suggested by several earlier workers.

The tribal disposition of *Camelina* is controversial, and there is little or no agreement among the several classifications consulted. The genus was placed in the Camelineae DC. (De Candolle, 1821, 1824; Bentham & Hooker), the Lepidieae DC. (Von Hayek, Janchen), and the Sisymbrieae DC. (Schulz). Although the placement of *Camelina* in the Alysseae is only a minor improvement, it is obvious that the boundaries of the Alysseae defined above are not natural and that this tribal disposition of the genus is not final.

Camelina is taxonomically troublesome, and only three species, *C. anomala, C. laxa* C. A. Meyer (Turkey, Iran, the Caucasus), and *C. hispida* Boiss. (Syria, Turkey, Iran) are distinct. The last is variable and contains three varieties (Hedge). The remaining species are weeds, and the boundaries between some of them are artificially drawn. Forms intermediate between *C. Rumelica* and *C. microcarpa* and between the latter and *C. sativa* have been found. *Camelina*

Alyssum (Miller) Thell., a weed of flax (*Linum usitatissimum* L.) fields in Europe said to be naturalized in the Dakotas and southern Canada, is completely interfertile with *C. sativa.* Their hybrids produce a very large array of intermediates found in nature (Tedin, 1925; Sinskaja & Beztuzheva). There is continuous variation in every character said to distinguish the two species. The nomenclature of the weedy camelinas can be quite misleading, and the number of species recognized has varied from seven (Vasil'chenko) to five (Meikle), four with several subspecies and varieties (Smejkal; Mirek, 1981; see both for extensive synonymy), and two (one of which has four subspecies) (Markgraf). In my opinion, *C. Rumelica, C. microcarpa,* and *C. sativa* are sufficiently distinct to merit specific status, but *C. Alyssum* should be treated as a subspecies of the last (as *C. sativa* subsp. *Alyssum* (Miller) E. Schmid). Interspecific hybridization has probably been responsible for blurring species boundaries, which otherwise are sharply defined in areas of allopatry. The pattern of continuous variation between species has been interpreted as a series of evolutionary differentiations from *C. microcarpa* to *C. sativa* and from the latter to *C. Alyssum* (Zinger). Both man's selection of flax (see below) and natural hybridization probably played major roles in creating the taxonomic complexity of the weedy camelinas.

Although most chromosome counts for *Camelina sativa* (including subsp. *Alyssum*) and *C. microcarpa* agree on $2n = 40$, counts of $2n = 26$ and $2n = 16$ and 32 have been reported for these species, respectively. Manton suggested that the base chromosome number for *Camelina* is eight and that all species are pentaploid, while others have believed that they are tetraploids based on ten. Stebbins, on the other hand, suggested that they may well be ancient allotetraploids, the ancestral species of which are unknown. Diploid counts of $2n = 12$ and $2n = 14$ are reported for *C. Rumelica* and *C. hispida,* respectively (Brooks; Goldblatt, 1984), but other counts ($2n$ = 24, 26, and 40) are also recorded for the former.

The chemistry of *Camelina* is poorly understood. The scant data indicate that both *C. sativa* and *C. microcarpa* contain 10-methylsulfinyldecylglucosinolate (Kjaer *et al.*). These species and *C. Rumelica* have uniform fatty-acid composition characterized by high concentrations (33–38 percent) of linolenic acid, by lower and nearly equal amounts (9–19 percent) of oleic, linoleic, and eicosenoic acids, and by negligible amounts (1–3 percent) of erucic acid (Kumar & Tsunoda).

The mode of origin of *Camelina* species as weeds of flax fields was studied by Zinger, Sinskaja & Beztuzheva, and Tedin (1925) and was reviewed by Hjelmqvist, Stebbins, and Barrett. According to these authors, certain forms of *C. sativa* (variously recognized as varieties, subspecies, or species) originated under selection pressures (climatic, phytosociological, agricultural—e.g., threshing and winnowing) operating in the cultivation of flax. Whether flax is grown for fiber or for seed oils, it is "mimicked" by plants of *C. sativa* in growth habit, branching pattern, internode length, leaf width, stem diameter and pubescence, flowering time, fruit dehiscence, and winnowing properties of the seeds. *Camelina sativa* subsp. *Alyssum* (listed in the literature as a distinct species or as a subordinate of *C. sativa* under the epithets *Alyssum, macrocarpa,* *foetida, dentata,* and *linicola*) scarcely grows outside flax fields, and it has evolved winnowing characteristics so similar to those of flax that their seeds remain mixed and are therefore resown the following season. Other aspects of *Camelina-Linum* relationships have been discussed by Stebbins and Barrett.

It has been shown that competition between *Camelina* and flax reduces the yield of the latter and produces in it smaller leaves, thinner stems, reduced branching, and smaller infructescences (Balschun & Jacob, 1961, 1972; Kranz & Jacob). Grümmer & Beyer demonstrated that the decline in productivity of flax is caused by allelopathic effects of leaf phenolic compounds (e.g., vanillic, p-hydroxybenzoic, and ferulic acids) washed from *Camelina* by rain. Others (e.g., Lovett and various co-workers) indicated that in the presence of certain free-living, nitrogen-fixing bacteria, aqueous washings of foliage of *C. sativa* (presumably containing toxic degradation products of isothiocyanates) stimulate the early growth of flax but inhibit its later growth and may cause marked ultrastructural changes in its root tips.

Species of *Camelina* accompanied the spread of agriculture in prehistoric times. Subfossil remains (as carbonized seeds) date back to the Neolithic and the Iron Age. *Camelina sativa* was cultivated for its stem fibers and edible oils by the Romans as early as 600 B.C. Despite the drastic decline in its cultivation, it is still grown in parts of Europe and the Soviet Union for the same purposes. The seeds contain 34–42 percent oil and about 33 percent protein. The seed oil has been used as an illuminant and for making soap, while the seed cake is fed to cattle.

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